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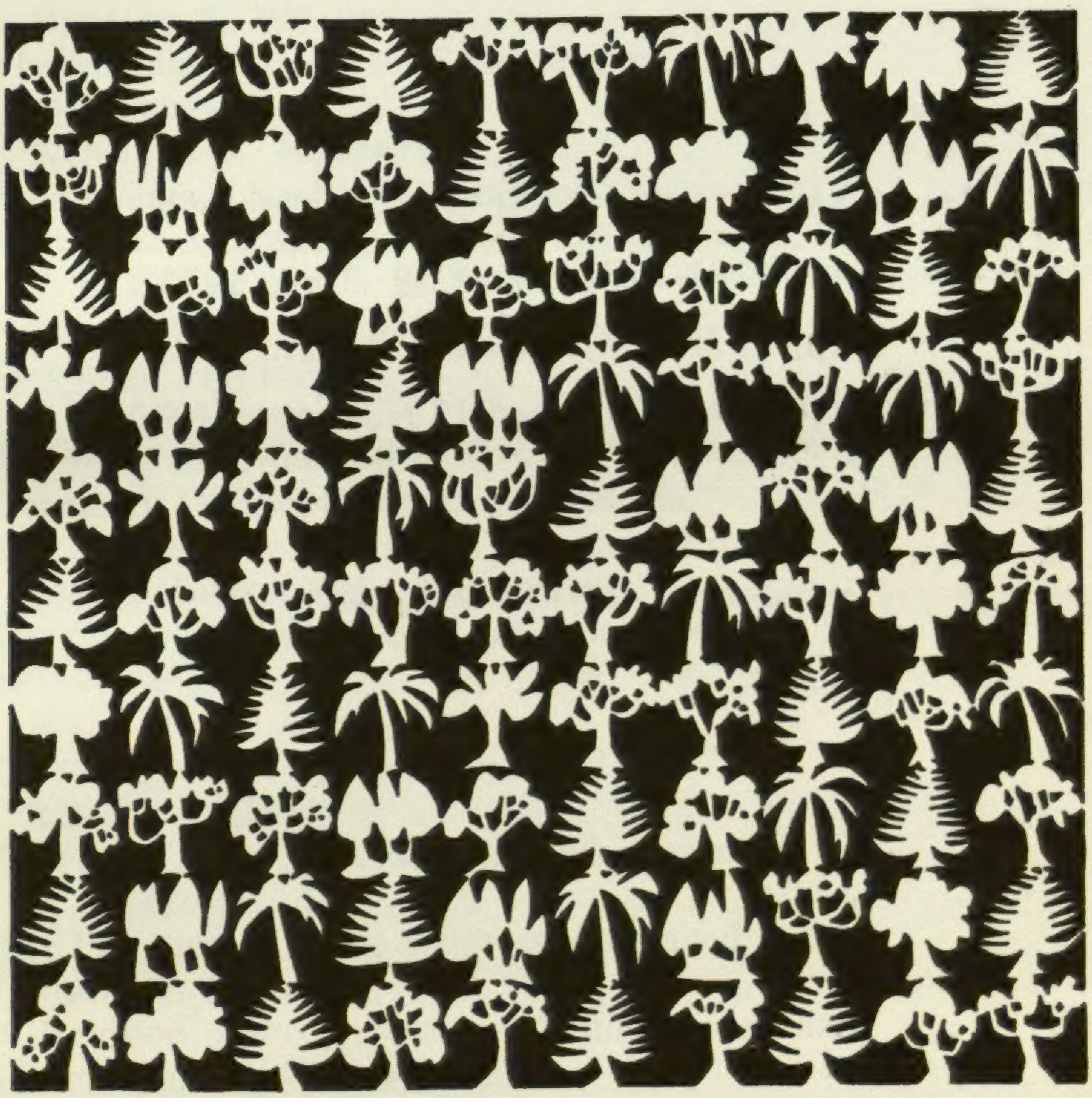

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COVER: A CENTURY OF TREES.

The cover design was planned and drawn by Karen Stoutsenberger Velmure especially for the *Journal of the Arnold Arboretum*. It will be used during 1972 to celebrate the Centennial Year of the Arnold Arboretum of Harvard University. The design consists of one hundred trees representing the range and diversity of the collections of the Arboretum.

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THE GENUS PIPER (PIPERACEAE) IN NEW GUINEA, SOLOMON ISLANDS, AND AUSTRALIA, 1

WEE-LEK CHEW

THIS PAPER, the first of a number to be published seriatim, is the outcome of an attempt to determine the collections made by the Royal Society Expedition to the Solomon Islands in 1965. It soon became clear in the investigation that reference had to be made to the New Guinean species of which more than one hundred have been described or recorded. Thus I was led to examine the very rich collections housed in the herbaria at Bogor (where types and authentic materials of earlier binomials are kept), Brisbane, Canberra, Lae, Singapore, and Sydney. In all, about 560 collections representing thirty-seven species have been studied. This resulted in twenty-two species being found conspecific with the fifteen dealt with in this paper. Also some of these have their ranges of distribution extended, while two Australian species have been found to be similar to New Guinean ones.

The presentation of the species in this series is very concise. Synonymy and literature references are kept at the minimum and descriptions are reduced to a diagnostic type. Detailed presentation is being reserved for the final comprehensive revision.

1. **Piper abbreviatum** Opiz in Presl, Rel. Haenk. 1: 157. 1828; Quisumbing, Philip. Jour. Sci. 43(1): 58. 1930.

P. bivalvantherum C.DC. Nova Guinea Bot. 8(2): 417. 1910, *syn. nov.*
P. internibaccum C.DC. *l.c.* 420. 1910, *syn. nov.*
P. fragrans Trelease, Jour. Arnold Arb. 9: 147. 1928, *syn. nov.*

TYPE. Philippine Islands. Luzon: *Haenke s.n.* (PR).
ICON.: Quisumbing, *l.c. fig. 24 & 25.* 1930.

Dioecious glabrous climbers. *Lamina* shortly petiolate, elliptic, ovate to broad ovate, ca. 10 cm. long, 5 cm. broad, length:breadth ratio ca. 2:1, glabrous on both sides; apex acute to acuminate; base cuneate to rounded, symmetrical; lateral veins 4 pairs, the lowermost pair very short, arising from the base, the 2nd and 3rd usually long, arising from the midrib

a little above the base, the distal 4th pair very short, often absent, arising from the midrib near the apex. *Stipules* to 1.5 cm. long, often shorter, usually as long as petioles. *Inflorescences* shorter than leaves, peduncular stalks ca. 1.5 cm. long, usually as long as petioles, males thin, to 6 cm. long, females shorter and thicker, ca. 2 cm. long, 0.8 cm. broad. *Male flowers* 2-staminate; stamens ca. 1 mm. long; anthers reniform to subglobose, 2-valved, slightly shorter than filaments; bracts peltate, subsessile, orbicular, the very short pedicel stout, hirsute. *Female flowers* sessile; stigmas 3- or 4-fid, sessile; bracts orbicular, peltate, sessile. *Fruits* sessile, entirely concrescent at maturity.

DISTRIBUTION. Philippines, Java, Celebes, Moluccas, New Guinea, Bismarck Archipelago, and Solomon Islands.

West New Guinea. SOUTHERN. Noord-rivier. Bivakeiland: *Versteeg 1058*, May (type of *P. bivalvantherum*, BO); *Versteeg 1021*, May (type of *P. internibaccum*, BO). VOGELKOP. Aifat River Valley: *van Royen & Sleumer 7052*, Oct. (LAE); Djitmau: *Versteegh BW. 7367*, May (CANB, LAE).

N.E. New Guinea. MOROBE DIST. Lae: *Millar GH 99*, March (BRI) & *NGF 9930* (BRI, LAE); Oomsis: *Brass 29201*, Apr. (CANB, LAE); *White NGF. 10474*, March (BRI, LAE); Wau-Salamaua Rd.; *Womersley & Millar NGF 8485*, Jan. (LAE).

Papua. CENTRAL DIV. Iawarere: *Brass 701*, Nov. (type of P. *fragrans*, BRI); near Sogeri: *Schodde 2927*, Sept. (BRI, LAE). MILNE BAY DIST. Dulubi village: *Henty NGF 16960*, June (BRI, CANB, LAE, NSW); Modewa: *Brass 28864*, Dec. (LAE). NORTHERN DIV. Pitoki village: *Hoogland 3973*, Sept. (BRI, CANB, LAE).

Bismarck Archipelago. NEW BRITAIN. Trans Vudal: *Streimann NGF 44396*, Aug. (LAE).

Solomon Islands. BOUGAINVILLE. Buin: *Kajewski 2047 & 2175*, Aug. (BRI, NSW); Lake Loloru: *Craven & Schodde 145*, July (BRI, CANB, LAE); *Lavarack & Ridsdale NGF 31475*, Feb. (LAE); *Schodde & Craven 3771*, Aug. (BRI, CANB, LAE).

Two types of leaf forms have been observed to occur in the individual plant. Leaves borne on the climbing stems are usually broad to very broad ovate with somewhat cordate bases. Those borne on free side branches tend to be narrow ovate to elliptic and often larger (e.g. *Schodde & Craven 3771* and *Kajewski 2047*). It is on such a variation that De Candolle's *P. bivalvantherum* and *P. internibaccum* as well as Trelease's *P. fragrans* are based.

The New Guinean and Solomon Islands' populations differ slightly from those in the Philippines. In the former, the lower part of the lamina is usually furnished with three pairs of lateral veins, the lowermost pair of which is often very short and faint. In the Philippine populations, however, the lowermost pair is altogether absent.

I am certain Rumphius' *Pharmacum magnum parvifolium* from Ternate, which Merrill (1917) failed to interpret, is referable to this species. The characteristic abbreviated infructescence and the venation of the small ovate leaves as clearly illustrated by Rumphius, leaves its identity in no doubt whatsoever.

Piper abbreviatum is not to be confused with *P. fragile* with which it has many characteristics in common (see note under that species).

2. **Piper aduncum** L. Sp. Pl. 29. 1753; C.DC. in DC. Prodr. **16**(1): 285. 1869.

Stephensia adunca (L.) Kunth, Linnaea **13**: 633. 1839.
Artanthe adunca (L.) Miq. Comm. Phyt. 49. *tab. 4.* 1840; Syst. Piperac. 449. 1844.

Icon.: Miq. *l.c. tab. 4.* 1840; Koord. Exk. Fl. Java **4**: 451. fig. *728.* 1924.

Monoecious shrubby trees. *Lamina* ovate, ca. 16 cm. long, 5 cm. broad, length:breadth ratio ca. 3:1, hispidulous; apex long acuminate; base lightly asymmetrically cordate; lateral veins 6–7 pairs arising alternately from the midrib, 1 or 2 short ones directly from the base. *Petiole* slightly longer than the sinus of the lamina base, shorter than the peduncular stalk. Inflorescences often bisexual, usually curved, as long as leaves, with flowers borne in dense spirals; peduncular stalk ca. 2 cm. long. *Male flowers* 2- or 3-staminate; bracts peltate, somewhat triangular. *Female flowers* sessile; stigmas 3-fid, sessile. *Fruits* sessile, obpyramidal, somewhat truncate.

Distribution. Mexico, Central America, northern South America, and West Indies. Naturalized in many places in Malesia.

West New Guinea. Northern. Hollandia. Polimac: *v.d. Sijde BW 4155*, Jan. (LAE). Waigeo Island. Majalibit Bay: *van Royen 5278*, Jan. (LAE).
N.E. New Guinea. Morobe Dist. Lae Botanic Gardens: *Native coll. NGF 4719*, Dec. (BO, BRI, LAE, NSW, SING); Huon Peninsula. Pindiu: *Hoogland 8847*, Apr. (BRI, CANB, LAE).

Being a native of the New World Tropics, this species bears no relationship whatsoever to any Malesian and Australasian native. Its closest American ally is *Piper hispidum* which has also been introduced into Java. From the few collections available for my study, *P. hispidum* seems to be only a less hispid version of *P. aduncum*.

I have made no comments on the type of *Piper aduncum*. Being a Linnaean species, based on pre-Linnaean ones, its typification is very involved, and can only be sorted out in the older herbaria of Western Europe where much pre-Linnaean literature and many collections are still extant. For the present work, I adopt the interpretation of Miquel and De Candolle.

3. **Piper amboinense** (Miq.) C.DC. in DC. Prodr. **16**(1): 347. 1869; Merrill Interpret. Herb. Amb. 182. 1917; Holth. & Lam, Blumea **5**: 173. 1942.

Chavica amboinensis Miq. Ann. Mus. Bot. Lugd. Bat. **1**: 134. 1863, incl. var. *latifolia* Miq. *l.c.* 140. 1863.

TYPE: Moluccas. Amboina: *Forsten*, May (L). FIGURE 1.

Dioecious climber, entirely glabrous. *Lamina* very shortly petiolate; ovate to oblong, somewhat rugose, 30 cm. long, 14 cm. broad, length: breadth ratio ca. 2:1; apex bluntly acuminate; base unilaterally cordate; lateral veins 4–5 pairs, the broader side often with 2 or 3 veins more, the two distal pairs arising from the midrib, the rest directly from the base. *Petioles* ca. 1 cm. long. Inflorescences shorter than leaves; peduncular stalks longer than petioles. *Male flowers* 2-staminate; anthers reniform,

FIGURE 1. **Piper amboinense.** ♀ twig, from type.

bracts peltate, rounded. *Female flowers* sessile; stigmas 3-fid, sessile. *Infructescences* often slightly longer than the leaves. *Fruits* sessile, somewhat cylindrical, free.

DISTRIBUTION. Celebes, Moluccas, and New Guinea.

Celebes. MAKASSAR PENIN. Pangkadjene: *Teysmann 11717* (BO).
Moluccas. AMBOINA. Batoe Gadjah: *Robinson Pl. Rumph. Amb. 58* (NSW); Ema: *Teysmann s.n.* (BO).
West New Guinea. Sine loc.: *Boorsma 2* (BO).

This species is very close to *Piper majusculum* from which it differs principally in the shorter female inflorescences, the less cordate lamina base, the very short petioles, and the fewer, differently patterned lateral veins.

The species has been erroneously recorded for Borneo by Holthuis and Lam (1942) who based their claim on one of Elmer's collections distributed as *Piper amboinense*. I have seen this collection and agree with Merrill (in Pl. Elm. Born. 40. 1929) that this is a misidentification. Elmer's specimen belongs to *P. majusculum*.

The New Guinean collection cited above seems to be not only the first record but also the only one for that island. I have included in the citation materials from Celebes and Moluccas as these collections had actually been authenticated by De Candolle and, as far as Teysmann's materials are concerned, actually by Miquel himself.

4. **Piper caninum** Bl. Verh. Bat. Genoot. **11**: 214. 1826; C.DC. in DC. Prodr. **16**(1): 341. 1869; Warb. Bot. Jahrb. **13**: 283. 1891; K. Sch. & Laut. Fl. Schutzgeb. 257. 1900.

Cubeba canina (Bl.) Miq. Syst. Piperac. 293. 1843.
P. banksii Miq. Versl. Med. Akad. ser. 9. **2**: 61. 1868; C.DC. Bot. Jahrb. **55**: 207. 1918; Benth. Fl. Austral. **6**: 205. 1873, *syn. nov.*
P. lauterbachii C.DC. in K. Sch. & Laut. Fl. Schutzgeb. 255. 1900, *syn. nov.*
P. macrocarpum C.DC. Nova Guinea Bot. **8**(2): 421. 1910, *syn. nov.*
P. pubipes C.DC. *l.c.* 421. 1910, *syn. nov.*
P. kietanum C.DC. Denkschr. K. Akad. Wiss. M.-N. Kl. Wien **89**: 527. 1914, *syn. nov.*
P. flavifructum Trelease, Jour. Arnold Arb. **9**: 147. 1928, *syn. nov.*

TYPE. Java: *Blume* (L).

ICON.: Bl. Verh. Bat. Genoot. **11**: *fig. 26.* 1826; Quisumbing, Philip. Jour. Sci. **43**(1): 121. *fig. 62.* 1930.

Dioecious climber. *Twigs* and petioles pilose. *Lamina* shortly petiolate, ovate, ca. 14 cm. long, 7 cm. broad, length:breadth ratio ca 2:1, glabrous on the upper side, subglabrous to pubescent on the lower side; apex long acute to acuminate; base slightly asymmetrically rounded to shallowly cordate; lateral veins 3–4 pairs, the distal pair arising from the midrib at ca. 2–3 cm. from the base, the rest directly from the base. *Petioles* ca.

2 cm. long. *Female inflorescences* up to as long as leaves, not densely flowered; peduncular stalk pilose, slightly longer than petioles. *Female flowers* sessile when young; stigma 4-fid, reflexed, sessile; bracts peltate, sessile. *Infructescences* often longer than leaves. *Fruits* ca. 4 × 3 mm. pedicellate, ovoid to globose.

DISTRIBUTION. Widely distributed in Malesia through New Guinea to the Solomon Islands and Australia.

West New Guinea. CENTRAL. Sabang: *Branderhorst 330* (isotype of *P. macrocarpum*, BO). Sine loc.: *Atasrip 64*, Exped. Wichmann (isotype of *P. pubipes*, BO); *Boorsma 4* (BO); *Branderhorst 425*, June (BO).

N.E. New Guinea. MADANG DIST. Aiome: *Frodin NGF 26954*, June (LAE). MOROBE DIST. Finschhafen: *Lauterbach 1337* (isotypes of *P. lauterbachii*, BO, BRI, SING); Oomsis: *Brass 29175*, April (LAE). SEPIK DIST. Ambunti: *Hoogland & Craven 10114*, May (BRI, LAE).

Papua. CENTRAL DIV. Dieni: *Brass 3926 & 3966*, May (BRI); Domara River: *Brass 1644*, June (isotype of *P. flavifructum*, BRI). MILNE BAY DIV. Normanby Island. Waikaiuna: *Brass 25390*, April (LAE).

Bismarck Archipelago. NEW BRITAIN. Gasmata: *Sayers NGF 24171*, March (LAE, NSW).

Solomon Islands. BOUGAINVILLE. Buin: *Kajewski 1782*, May (BRI). GUADALCANAL. Mt. Tutuve: *Kajewski 2646*, May (BRI). NEW GEORGIA. Vaimbu River: *Cowmeadow BSIP 4762*, Sept. (LAE). SAN CRISTOBAL. Maru Bay: *Gafui BSIP 12829*, Nov. (LAE).

Australia. QUEENSLAND. Cape Tribulation: *Mason s.n.*, July (NSW); Rockingham Bay: *Dallachy s.n.* (BO, NSW).

This widespread and consequently very well known species needs no introduction. Though quite variable in lamina form and infructescence size, it is easily recognized throughout its entire range of distribution. I have examined the types and authenticated materials of the synonyms cited above and have found that they come within the circumscription of this species as established by Blume and adopted by De Candolle and subsequent authors.

5. **Piper decumanum** [Rumph.] Linnaeus in Stickman, Herb. Amb. 19. 1754; Amoen. Akad. **4**: 128. 1759; Merrill, Interpret. Herb. Amb. 181. 1917.

Sirium decumanum Rumph. Herb. Amb. **5**: 45. *tab. 27*. 1747.
Chavica majuscula (Bl.) Miq. Syst. Piperac. 271. 1843, *partim*.
Ch. imperialis Miq. Ann. Mus. Bot. Lugd. Bat. 1: 134, 140. 1863.
Ch. rumphii Miq. *l.c.* 141. 1863.
P. forstenii C.DC. in DC. Prodr. **16**(1): 348. 1869; Nova Guinea Bot. 8(6): 1007. 1914; Gibbs. Phyt. Fl. N. Guinea 207. 1917.
P. rumphii (Miq.) C.DC. in DC. Prodr. **16**(1): 354. 1869.
P. majusculum auct. *non* Bl., C.DC. *ibid*. 350. 1869, *partim*.

TYPE. Moluccas: *Rumph. Herb. Amb. 5: tab. 27*. 1747.

ICON.: Rumph. *l.c.*; Quisumbing, Philip. Jour. Sci. **43**(1): 43. *fig. 14.* 1930.

Dioecious climber, completely glabrous. *Lamina* very shortly petiolate, ovate, often rugose, ca. 40 cm. long, 18 cm. broad, length:breadth ratio ca. 2:1; apex acute to bluntly acuminate; base asymmetrically cordate to auriculate; lateral veins 4–6 pairs, the distal pair arising alternately from the midrib, the rest from the base, the larger side usually with 2–3 veins more. Petioles often shorter than the auriculate base, sheathing at the lower half. *Male inflorescences* about as long as the leaves. *Female inflorescences* much longer; peduncular stalks as long as petioles. *Female flowers* sessile; stigmas 2-lipped to 3-fid, borne on tapering styles. *Infructescences* to 60 cm. long. *Fruits* ca. 3 × 1.5 mm., oblong, sessile, congested.

DISTRIBUTION. Philippine Islands, Celebes, Moluccas, and New Guinea.

West New Guinea. NORTHERN. Sawaii: *Gjellerup 599*, Aug. (BO). VOGELKOP PENINSULA. Manokwari: *Schram BW 12924*, March (LAE). WAIGEO ISLAND. Radjah Ampat: *van Royen 5215*, Jan. (CANB, LAE).

N.E. New Guinea. MADANG DIST. near Aiome: *Womersley NGF 24752*, June (LAE). SEPIK DIST. Ossima: *Streimann & Kairo NGF 39196*, Jan. (LAE).

Linnaeus based *Piper decumanum* entirely on Rumphius' *Sirium decumanum* from the Moluccas. Unfortunately, he later (1762) extended the concept to include an entirely different species described by Plumier from the American Tropics: unfortunately, because this led to some confusion on the use of the name *P. decumanum*.

The error was noticed by Miquel (1843) and De Candolle (1869) who quite rightly separated Plumier's species from the Moluccan one; but both erred in other respects. They incorrectly retained the epithet for the American species and placed our Moluccan one under *Piper majusculum*, an entirely different species (see notes there). It was not until 1917 that the matter was corrected by Merrill.

The basal leaves of this species differ greatly from the upper ones in being almost symmetrically ovate with deeply symmetrically cordate bases. Both *Sirium decumanum* of Rumphius and *Chavica rumphii* of Miquel are based on plants with such leaves.

I have seen authenticated materials of *Piper forstenii*, under which name De Candolle recorded our species from New Guinea, and I am satisfied that *P. forstenii* was correctly referred to *P. decumanum* by previous authors.

6. **Piper fragile** Benth. Lond. Jour. Bot. **2**: 234. 1843; C.DC. in DC. Prodr. **16**(1): 358. 1869; Nova Guinea Bot. **8**(2): 417. 1910.

Chavica benthamiana Miq. Syst. Piperac. 233. 1843.

TYPE. New Guinea: *Hinds s.n.* (K).

ICON.: Quisumbing, Philip. Jour. Sci. **43**(1): 100. *fig. 50.* 1930.

Dioecious climber, entirely glabrous. *Lamina* shortly petiolate, ovate, ca. 8 cm. long, 6 cm. broad, length:breadth ratio ca. 4:3; apex acute; base rounded, often subpeltate, rather coriaceous; lateral veins 2 pairs, often with one more very short and faint pair at the very base, all arising from the base. *Petioles* ca. 1/4 the length of lamina. *Inflorescences* shorter than leaves; the females very short; densely flowered in both; peduncular stalks as long as petioles; bracts peltate, sessile. *Male flowers* with 2 stamens; filaments very short, oblong; anthers ovoid, as long as filaments, 2-valved. *Female flowers* sessile; stigmas 4-fid, reflexed, sessile. *Infructescences* shorter than leaves, often congested and curved. *Fruits* ca. 3 mm. diam., almost globose, concrescent at the lower half.

DISTRIBUTION. Philippines, Moluccas, New Guinea, and Solomon Islands.

West New Guinea. Sine loc.: *Boorsma 9* (BO).
N.E. New Guinea. MADANG DIST. Bagabag Island: *Vandenberg & Mann NGF 42263*, June (LAE); Serang: *Millar NGF 37693*, July (LAE). WEST SEPIK DIST. Selio Island: *Millar & Vandenberg NGF 40900*, June (LAE).
Papua. MILNE BAY DIV. Wagalasa Island: *Mann & Osborn NGF 43037*, March (LAE).
Solomon Islands. BOUGAINVILLE: *Kajewski 1595*, March (BRI). GUADALCANAL. Rove West: *Nakisi BSIP 7919*, June (LAE); *Corner RSS 193*, NOV. (SING).

This species can easily be confused with *Piper abbreviatum* with which it has a few characteristics in common. In both, the lamina are small and ovate with few veins, the female inflorescences rather short and "abbreviated," and the fruits concrescent. A detailed examination of these characters, however, reveals important differences between the two species. In *P. fragile*, all the lateral veins arise from the very base which is often subpeltate; whereas in the other species this is not so. In the female flowers and fruits, the sigmas are 3-fid and the fruits entirely concrescent in *P. abbreviatum*; but they are 4- or 5-fid and the fruits only partially concrescent in *P. fragile*.

Piper varibracteum C.DC. (1910) of the Philippines probably is a synonym of *Piper fragile*, but the type material of it must be examined before its relationship to *P. fragile* can be assessed with certainty.

7. **Piper gibbilimbum** C.DC. Nova Guinea Bot. **8**(2): 416. 1910; Bot. Jahrb. **55**: 211. 1918.

P. squamuliferum C.DC. Nova Guinea Bot. 8(6): 1009. 1914, *syn. nov.*

TYPE. West New Guinea. Noord-rivier, near Alkmaar: *Versteeg 5115*, July (BO). FIGURE 2.

Dioecious trees. *Lamina* very shortly petiolate, asymmetrically ovate, ca. 15 cm. long, 9 cm. broad, length:breadth ratio ca. 3:2 to 5:3, generally glabrous, sometimes lightly hirsute on the veins on the under side, brown puncticulate on both surfaces; apex acuminate; base unilaterally

FIGURE 2. **Piper gibbilimbum.** A, ♀ twig; B, stigma, from *Brass 12252.*

to asymmetrically cordate, those of the basal leaves usually deeply symmetrically cordate; lateral veins 3 or 4 pairs, all arising from the base, the broader side often with one more faint vein. *Stipules* thin, ca. 2 cm. long, usually as long as petioles. *Inflorescences* usually shorter than adult leaves; peduncular stalks usually as long as petioles, male and female equal in length. *Male flowers* 2-staminate; stamens ca. 0.4 mm. long;

anthers reniform, 2-valved, on extremely short filaments; bracts orbicular, subsessile, peltate, the very short pedicel lightly hirsute. *Female flowers* sessile; stigmas 3-fid, sessile; bracts long pedicellate, peltate, orbicular, the pedicel very lightly hirsute. *Fruits* sessile, free, crowded.

DISTRIBUTION. New Guinea.

West New Guinea. NORTHERN. Balim River: *Brass 11671*, Dec. (BO); Idenburg River: *Brass 12252*, Jan. (BO, BRI). SOUTHERN. Noord-rivier. Alkmaar: *Versteeg 1515*, July (type of *P. gibbilimbum*, BO); Mt. Hellwig: *Roemer 1268* (type of *P. squamuliferum*, BO); Wissel Lakes: Enarotali: *Vink & Schram BW 8593*, May (LAE).

N.E. New Guinea. EASTERN HIGHLANDS. Chimbu Divide: *Womersley et al. NGF 6097*, Nov. (BRI, LAE); Kundiava: *Millar & Nicholson NGF 13847*, Sept. (BRI, CANB, LAE, NSW). MADANG DIST. Kar Kar Isl.: *Mann & Vandenberg NGF 43192* (LAE). MOROBE DIST. Edie Creek: *Millar & Holttum NGF 15824*, Aug. (BRI, LAE, NSW); Kikiepa: *Womersley & Thorne NGF 11860*, May (BRI, BO, CANB, LAE, NSW). SEPIK DIST. Bliri River: *Darbyshire & Hoogland 8254*, July (BO, CANB, LAE); Oksapmin: *Henty et al. NGF 38972*, Oct. (BRI, LAE, NSW). WESTERN HIGHLANDS. Nondugl: *Womersley NGF 4349*, April (BRI, LAE).

Papua. MILNE BAY DIST. Maneau Range: Mt. Dayman: *Brass 23235*, July (CANB, LAE). SOUTHERN HIGHLANDS. Kuave: *Pullen 2778*, July (LAE); Lake Kutubu: *Gray NGF 8109*, May (BRI, LAE, NSW); *Schodde 2355*, Sept. (LAE).

Piper squamuliferum belongs to this species. The presence of bracts at the base of the ovary, a characteristic claimed to be exclusive to *P. squamuliferum*, has also been observed in *P. gibbilimbum*, though not as constantly as in the former species.

This tree species is one of the very successful colonizers of disturbed forests in New Guinea. Spread over an altitudinal range of from 800 to 2600 meters, it is found to be particularly common at about the 1500 meter contour.

Piper gibbilimbum is close to *P. plagiophyllum* from which it can be distinguished by the different venation pattern and the longer peduncular stalks.

8. **Piper macropiper** Pennant, Outl. Globe **4**: 242. 1800; Merrill, Jour. Arnold Arb. **29**: 191. 1948.

Sirium arborescens tertium Rumph. Herb. Amb. **5**: 46. *tab. 28, fig. 1*. 1747.
P. arborescens Rumph. Roxb. Hort. Beng. 80. 1814, Fl. Ind. **1**: 161. 1820; Miq. Syst. Piperac. 320. 1844; C.DC. in DC. Prodr. **16**(1): 358. 1869; Merrill, Interpret. Herb. Amb. 180. 1917.
P. miniatum Bl. Verh. Bat. Genoots. **11**: 166. 1826; K. Sch. & Laut. Fl. Schutzgeb. 261. 1900; C.DC. Nova Guinea Bot. **8**(2): 415. 1910.
Chavica miniata (Bl.) Miq. Syst. Piperac. 234. 1843.
P. pendulum Warb. Bot. Jahrb. **13**: 283. 1891, *syn ?*
P. quinquenervium Warb. *l.c.* 284. 1891, *syn.?*
P. brassii Trelease, Jour. Arnold Arb. **9**: 147. 1928, *syn. nov.*
P. morianum Trelease, *l.c.* 148. 1928, *syn. nov.*

TYPE. Moluccas: *Rumph. Herb. Amb. 5: tab. 28, fig. 1.* 1747.

ICON.: Bl. Verh. Bat. Genoots. 11: *fig. 6.* 1826, as *P. miniatum*; Miq. Illus. Piperac. *tab. 28.* 1847, as *C. miniata*; Quisumbing, Philip. Jour. Sci. 43(1): 21. 1930, as *P. arborescens.*

Dioecious climber; nodes often thickened. *Lamina* very shortly petiolate; ovate, ca. 16 cm. long, 6 cm. broad, length:breadth ratio from 2:1 to 5:2, glabrous on the upper side, glabrous to pubescent on the lower; apex acuminate; base round to shallowly cordate, very slightly asymmetrical, one side often produced into a minute auricle; lateral veins 2 or 3 pairs arising from the base, prominent. *Stipules* to 2 cm. long, early caducous. *Inflorescences* much longer than the leaves, often to 20 cm.; peduncular stalks ca. 3 cm. long. *Male flowers* 2- or 3-staminate; stamens very short; anthers reniform, 2-valved, often appearing truncate. *Female flowers* sessile, free, crowded; stigmas 3-fid, sessile. *Fruits* sessile, ovoid to oblong, crowded, not concrescent at maturity.

DISTRIBUTION. Widely distributed from India, Ceylon through Malesia and New Guinea to the Solomon Islands in Melanesia.

West New Guinea. NORTHERN. Idenburg River: *Brass 13710 & 13976*, Jan. (BRI).

N.E. New Guinea. MOROBE DIST. Finschhafen: *Hellwig 624*, Apr. (BO); *Lauterbach 1489* (BO, BRI); near Mumeng: *Hartley 9765*, Jan. (BRI, CANB, LAE, NSW). EASTERN HIGHLANDS. Kainantu: *Henty NGF 29361*, March (BRI, CANB, NSW).

Papua. CENTRAL DIV. Iawarere: *Brass 683*, Nov. (isotype of *P. brassii*, BRI); Mori River: *Brass 1562*, May (isotype of *P. morianum*, BRI).

Solomon Islands. BOUGAINVILLE. Buin: *Craven & Schodde 201*, Aug. (BRI, LAE); *Kajewski 2133*, Aug. (BO, BRI, NSW, SING). GUADALCANAL. Tutuve Mts.: *Kajewski 2579*, Apr. (BRI). SAN CRISTOBAL. Waimamura: *Brass 2581, Aug.* (BRI). SANTA YSABEL. Meringe: *Brass 3347*, Dec. (BO, BRI); *Whitmore BSIP 2257*, Oct. (LAE).

Variation in size, shape and vestiture of the lamina and twig is great in *Piper macropiper.* The length of the lamina, for instance, varies from 8 to 20 cm. In shape, the lamina can be very narrowly to very broadly ovate with a fairly noticeable cordate base. As for vestiture, the variation extends from completely glabrous to fairly densely pubescent. As all manner of gradations have been observed between the extremes, and as many of these variations have actually been observed to occur on an individual, Trelease's species as well as the numerous varieties recognized by previous authors are not maintained here. Nevertheless, this species remains one of the most distinctive in the genus.

In the Herbarium at Bogor, Indonesia, there is a collection of Lauterbach *no. 1489* and one of Hellwig *624* named by De Candolle as *Piper pendulum* and *P. quinquenervium* respectively. These collections have been found by me to belong to *Piper macropiper*, and the names they bear are placed in the synonymy above, each with a query because their types have not been examined.

This species has suffered two name changes, the latest of which is most unfortunate because it was caused by the discovery of an overlooked publication (*vide* Merrill 1948).

9. **Piper majusculum** Bl. Verh. Bat. Genoots. 11: 210. 1826; C.DC. in DC. Prodr. 16(1): 350. 1869, partim; Quisumbing, Philip. Jour. Sci. 43(1): 45. 1930.

Chavica majuscula (Bl.) Miq. Syst. Piperac. 271. 1843, *partim*.
P. insignilimbum C.DC. Candollea 2: 219. 1925, *syn. nov.*

TYPE. Java. Mt. Salak: *Blume* (L).

ICON.: Bl. Verh. Bat. Genoots. 11: *fig. 25*. 1826; Quisumbing, Philip. Jour. Sci. 43(1): 46. *fig. 16*. 1930.

Dioecious climber. *Lamina* shortly to very shortly petiolate, ovate to pentagonal, ca. 30 cm. long, 15 cm. broad, length-breadth ratio ca. 2:1, sparsely hirsute on the midrib below; apex shortly acuminate; base asymmetrically cordate, one or both sides auriculate; lateral veins ca. 6 pairs, all arising from the midrib, the auricles usually with 2–3 more short and rather faint veins arising from the base. *Petioles* ca. 2 cm. long, usually shorter than the sinus of the lamina base. *Inflorescences* very much longer than leaves, very densely flowered; peduncular stalks longer than petioles. *Female flowers* sessile; stigmas 3-fid, sessile; bracts peltate, sessile, glabrous. *Infructescences* ca. 35 cm. long, 2 cm. diam., pendulous. *Fruits* concrescent.

DISTRIBUTION. Widely distributed in Malesia, through New Guinea to the Solomon Islands.

West New Guinea. BIAK. Oregontrail: *Vink BW 12052*, July (CANB, LAE). VOGELKOP PENINSULA. Manokwari: *Versteegh BW 7572*, April (LAE); Nabire: *Kanehira & Hatusima 11531 & 12643* (BO). Sine loc.: *Boorsma 3 & 13* (syntypes of *P. insignilimbum*, BO).

Papua. GULF DIV. Kikori. Biara: *Gray & Floyd NGF 8050*, July (BRI, LAE).

Solomon Islands. GUADALCANAL. Mt. Mambulu: *Nakisi BSIP 7914*, June (LAE). SANTA YSABEL. Maloku: *Beer BSIP 7259*, May (LAE).

I have examined the holotype of *Piper insignilimbum* and having compared it with authentic materials of Blume's species, I am quite satisfied that it is conspecific with *Piper majusculum*. The only difference I can find between the two is in the petiole which seems to be slightly shorter in the New Guinea and Solomon Island plants.

It is not surprising that Miquel and De Candolle confused Rumphius' *Sirium decumanum* (= *Piper decumanum*) with *Piper majusculum*. In the first place, the lamina of the latter are rather similar to the basal leaves of *P. decumanum* in that both are cordate and often auriculate at the base. Rumphius' illustration clearly depicts a plant with such basal leaves. Secondly, both species are notable by their greatly elongated female inflorescences which, being densely covered with flowers, become

pendulous at maturity. The two species, however, differ clearly in the following characters: (a) the stigmas in *P. majusculum* are 3-fid, small and sessile, in *P. decumanum* they are 2-lipped or 3-fid and borne on tapering styles, (b) the fruits are concrescent in *P. majusculum* but free in *P. decumanum*.

10. **Piper mestonii** Bailey, Rep. Exped. Bellenden-Ker 54. 1889; Lam, Vegetationsbilder **15**(5/6): 5. 1924.

P. rueckeri K. Sch. & Hollrung, Fl. Kais. Wilh. Land. 36. 1889; C.DC. Bot. Jahrb. **55:** 204. 1918, *syn. nov.*
P. bilobulatum C.DC. Nova Guinea Bot. 8(2): 418. 1910, type only, *syn. nov.*
P. rhodocarpum Trelease, Jour. Arnold Arb. **9:** 149. 1928, *syn. nov.*

TYPE. Australia. Queensland. Harvey's Creek. Russell River: *Meston & Bailey s.n.* (isotype of *P. mestonii*, NSW).

ICON.: Bailey, Compr. Cat. Queensl. Pl. *tab. 12, fig. 402*. 1913.

Dioecious climber. *Twigs* glabrous, nodes fairly prominent. *Lamina* moderately petiolate, ovate, ca. 20 cm. long, 14 cm. broad, length:breadth ratio ca. 3:2, glabrous; apex acute to bluntly acuminate; base rounded to cordate at maturity; lateral veins ca. 4 pairs, the distal pair arising alternately ca. 1/3 up the midrib, the 2nd pair slightly above the base, the rest directly from the base. *Stipules* much shorter than petioles. *Inflorescences* shorter than leaves, peduncular stalks glabrous, as long as petioles; males thinner and shorter; bracts orbicular, sessile. *Female flowers* sessile; stigmas 2-lipped, on long attenuate styles. *Infructescences* ca. 12 cm. long, 1.5 cm. diam., brick red at maturity. *Fruits* sessile, completely concrescent at maturity.

DISTRIBUTION. New Guinea and Australia.

West New Guinea. NORTHERN. Begowri: *Gjellerup 219*, June (BO); Hollandia: *Kalkmann BW 3420*, March (CANB, LAE); *Koster BW 1175*, Jan. (CANB, LAE). SOUTHERN. Noord-rivier. Alkmaar: *Versteeg 1533*, Aug. (isotype of *P. bilobulatum*, BO).

N.E. New Guinea. MOROBE DIST. Umi River. Kalapit: *Millar & van Royen NGF 15658*, Jan. (BRI, CANB, LAE, NSW). MADANG DIST. Bili Bili River: *Hoogland 4847*, June (BRI, CANB, LAE). SEPIK DIST. Augustafluss: *Hollrung 260* (isotype of *P. rueckeri*, BO); Leitre: *Millar & Vandenberg NGF 40944*, June (LAE).

Papua. CENTRAL DIV. U-uma River: *Brass 1427*, May (isotype of *P. rhodocarpum*, BRI). WESTERN DIV. Fly River: *Brass 8276*, Nov. (BRI, CANB); Palmer River: *Brass 7258*, July (BRI).

Australia. QUEENSLAND. Cairns Dist. Harvey Creek: *Flecker 12449*, Aug. (NSW); *Meston & Bailey s.n.* (isotype of *P. mestonii*, NSW).

I am confident that this New Guinean species, *Piper mestonii*, is none other than the Queensland Long Pepper of Australia which Lam (1924) recorded as being very common along rivers in New Guinea. I have examined all the type materials of the names listed above in synonymy and have found that they differ from each other only in lamina form.

The type of *Piper rueckeri* has ovate leaves, that of *P. bilobulatum* narrowly ovate to small elliptic leaves with very cuneate bases, while *P. rhodocarpum* has lamina more cordate than *P. mestonii*. As numerous rerecent collections have been found to contain all these lamina forms on one plant (e.g. *Schiefenhovel 107*; *Hoogland & Craven 10575, & Pullen 2818*), it is here concluded that these leaf forms are but manifestations of the various developmental stages in the life history of one species.

There is a superficial resemblance between *Piper mestonii* and *P. versteegii*, particularly in lamina shape, size, and venation. Because of this, De Candolle misidentified Gjellerup's collection no. 219 as *P. versteegii* (*vide*: C.DC. Nova Guinea Bot. 8(6): 1007. 1914). The two species are however quite distinct (see notes under *P. versteegii*) and are easily told apart by many other characters as was done by De Candolle subsequently in 1923 in his monographic key.

Piper mestonii seems close to *P. reinwardtianum* of the Moluccas from which it differs only in the stigmas being 2-lipped instead of 3- or 4-fid.

The Papuans call this species "O–O–O"!

11. **Piper plagiophyllum** K. Sch. & Laut. Fl. Schutzgeb. 260. 1900; C.DC. Bot. Jahrb. **55**: 206. 1918; Ridl. Trans. Linn. Soc. Bot. ser. 2. **9**: 143. 1916.

TYPE. N.E. New Guinea. Oertzen Gebirge: alt. 300 meters, *Lauterbach 2143*, May (B). FIGURE 3.

Dioecious trees ca. 5 meters high, entirely glabrous. *Lamina* very shortly petiolate, asymmetrically ovate, ca. 17 cm. long, 10 cm. broad, length:breadth ratio ca. 3:2; apex short acuminate; base asymmetrically rounded to unilaterally cordate, the lower ones properly cordate; lateral veins 4 pairs, the distal pair arising alternately from the midrib, the rest from the base, the lowermost pair usually very short and faint. *Stipules* 4–5 cm. long, much longer than petioles. *Inflorescences* of equal length in both sexes, much shorter than adult leaves, but longer than petioles; peduncular stalks very short, less than 1 cm. *Male flowers* 2-staminate; stamens ca. 1 mm. long; anthers reniform, large, longer than filaments; bracts orbicular, peltate, sessile, hirsute at the base. *Female flowers* sessile; stigmas 3-fid, sessile; bracts as in the males. *Fruits* sessile, free, crowded.

DISTRIBUTION: New Guinea.

West New Guinea. VOGELKOP PENINSULA. Arfak Mts.: *Versteegh BW 12665*, May (LAE).

N.E. New Guinea. MOROBE DIST. Busu River: *Hartley 12187*, Sept. (BRI, CANB, LAE); Busu Road: *Henty NGF 11912*, Feb. (BO, CANB, LAE, NSW); Butibum River: *Hartley 9620*, Dec. (BRI, CANB, LAE); Kaindi: *Brass 29542*, May (CANB); Rebel: *Schlechter 16791* (BO); Mt. Torricelli: *Schlechter 14604* (BO); Wobbe: *Schlechter 16252* (BO).

Papua. MILNE BAY DIV. between Agamoia & Ailuluai Mts.: *Brass 27128*,

FIGURE 3. **Piper plagiophyllum.** ♀ twig, from *Henty NGF 11912.*

June (LAE). Goodenough Island: *Brass 24735*, Oct. (LAE). Kako: *Weinland 256* (BO, BRI).

Another tree species, *Piper plagiophyllum* is also found to be common, particularly in disturbed habitats or abandoned gardens. It has quite a broad altitudinal range, from sea level to about 2,000 meters, and is especially abundant in damp areas at about the 1,000-meter contour.

Schumann and Lauterbach compared this species with *Piper betle* although they admitted that the two species differ markedly from each other in habit of growth and shape of lamina. Our species is actually very close to *P. gibbilimbum* from which it differs in two characters, one pair of lateral veins issues from the midrib, and the peduncular stalks are extremely short.

12. **Piper sclerophloeum** C.DC. Denkschr. K. Akad. Wiss. M.-N. Kl. Wien 89: 530. 1914, includ. var. *scandens* C.DC. *l.c.*

TYPE. Solomon Islands. Buka, prope pagum Jeta, septembri, *K. et L. Rechinger 4387* (W).

ICON.: C.DC. *l.c.* 530. *tab. 4, fig. 6a.* 1914.

Dioecious, climbing, often erect. *Twigs* glabrous at maturity. *Lamina* moderately petiolate, asymmetrically ovate, ca. 23 cm. long, 16 cm. broad, length:breadth ratio ca. 4:3, the upper side glabrous, the lower side hirtellous on veins, soon glabrous; apex shortly acuminate or acute; base asymmetrically rounded to unilaterally cordate; lateral veins 4 pairs, the distal pair alternate, arising ca. 3 cm. up the midrib, the 2nd pair at ca. 1 cm. and the rest arising from the base, the broader side often with one more vein. *Petioles* ca. 3 cm. long, usually equalling stipules. *Inflorescences* shorter than leaves, with peduncular stalks shorter than petioles; the males ca. 10 cm. long, 0.6 cm. diam., the females 7 cm. long, 1.5 cm. broad. *Female flowers* sessile; stigma bifid, borne on gradually tapering styles. *Fruits* sessile, not concrescent.

DISTRIBUTION: Solomon Islands.

Solomon Islands. BOUGAINVILLE. Buin: *Craven & Schodde 513*, Sept. (BRI, LAE); Kieta: *Kajewski 1585*, March (BO, NSW, SING); Urugu: *Kajewski 2185*, Oct. (BRI); Tutuve Mts.: *Kajewski 2598*, April (BRI); Pavairi: *Lavarack & Ridsdale NGF 31239*, Jan. (BRI, LAE, SING). CHOISEUL. Solovae Inlet: *Whitmore BSIP 3917*, April (LAE). GUADALCANAL. Duidui Area: *Fa'arodo BSIP 12116*, Oct. (LAE); *Sirute BSIP 10091*, June (LAE). SAN CRISTOBAL. Waimamura: *Brass 2577, 2583, & 3139*, Aug.–Sept. (BRI). SANTA YSABEL. Tiratona: *Brass 3345*, Dec. (BO, BRI).

This species is reported to be common in both primary and secondary forests below 1,000 meters in altitude. Kajewski recorded the plants as robust climbers that often grow into shrubby trees needing no support. For this reason, De Candolle's variety *scandens* is not maintained.

The shape of the leaf-base varies considerably in this species. While

most of the collections studied have unilaterally cordate bases, a number of them have been observed to have bases which range from asymmetrically rounded to fairly deeply cordate.

Our species resembles somewhat *P. mestonii* from which it differs in: (1) fruits not concrescent, (2) peduncular stalks shorter than petioles, and (3) lamina generally asymmetrical.

13. **Piper stenocarpum** C.DC. Ann. Cons. Jard. Bot. Genève 2: 270. 1898.

TYPE. Papua. Central Div. Mt. Yule: *G. Belford ?*, Dec. 1890, *MEL 1010379* (MEL). FIGURE 4.

Dioecious climber, entirely glabrous. *Lamina* very shortly petiolate, ovate to narrowly ovate, ca. 13 cm. long, 5 cm. broad, length:breadth ratio ca. 5:2; apex long acuminate; base usually asymmetrical, the shorter side cuneate, the other rounded; lateral veins 2 or 3 pairs, the distal pair arising from the midrib 2–3 cm. from the base, the second also from the midrib very near the base, the basal pair, if present, always from the base and usually very faint. *Stipules* very small. *Inflorescences* longer than leaves, very slender, especially the males; peduncular stalks much longer than petioles; bracts sessile, somewhat oblong. *Male flowers* 2-staminate; filaments much longer than anthers at maturity. *Female flowers* sessile; stigmas very short and bluntly 2-lipped, on long attenuate styles. *Infructescences* to 20 cm. long, 1 cm. diam., bright red at maturity. *Fruits* sessile, completely concrescent at maturity.

DISTRIBUTION. New Guinea.

N.E. New Guinea. CENTRAL HIGHLANDS. Korofunota: *Womersley & Floyd NGF 6934*, Nov. (BRI, LAE). EASTERN HIGHLANDS. Daulo: *Pullen 407*, Aug. (CANB, LAE). MOROBE DIST. Aiewa: *Streimann & Kairo NGF 39034* (LAE); Finnesterre Mt.: *Womersley & Thorne NGF 11891* (BRI, LAE). SEPIK DIST. Nerenanip village: *Frodin NGF 28509*, Sept. (LAE). WESTERN HIGHLANDS. Mt. Kum: *Womersley NGF 43611*, March (LAE).

Papua. CENTRAL DIV. Mt. Albert Edward: *van Royen NGF 30092*, Jan. (BRI, LAE); Mt. Yule: *MEL 1010379, coll. G. Belford ?* (type, MEL). MILNE BAY DIST. Goodenough Island: *Brass 25014*, Oct. (LAE). NORTHERN DIV. above the Gap: *Carr 13793 & 13815*, Dec. (CANB). SOUTHERN HIGHLANDS. Near Kiburu: *Schodde 1397* (LAE).

Piper stenocarpum is clearly a highland relative of *P. mestonii*, the Queensland Long Pepper now found to be common in the lowlands and foothills of mountains in New Guinea. The characteristics that the two species have in common are the thin and long male inflorescence, the stamens borne on fairly thick and elongated filaments, the stigmas 2-lipped and borne on long attenuate styles, and the fruits completely concrescent at maturity. They are, however, easily distinguished from each other thus: in *P. stenocarpum* the inflorescences are much longer than the leaves, the peduncular stalks longer than petioles, and the stigma very shallowly 2-

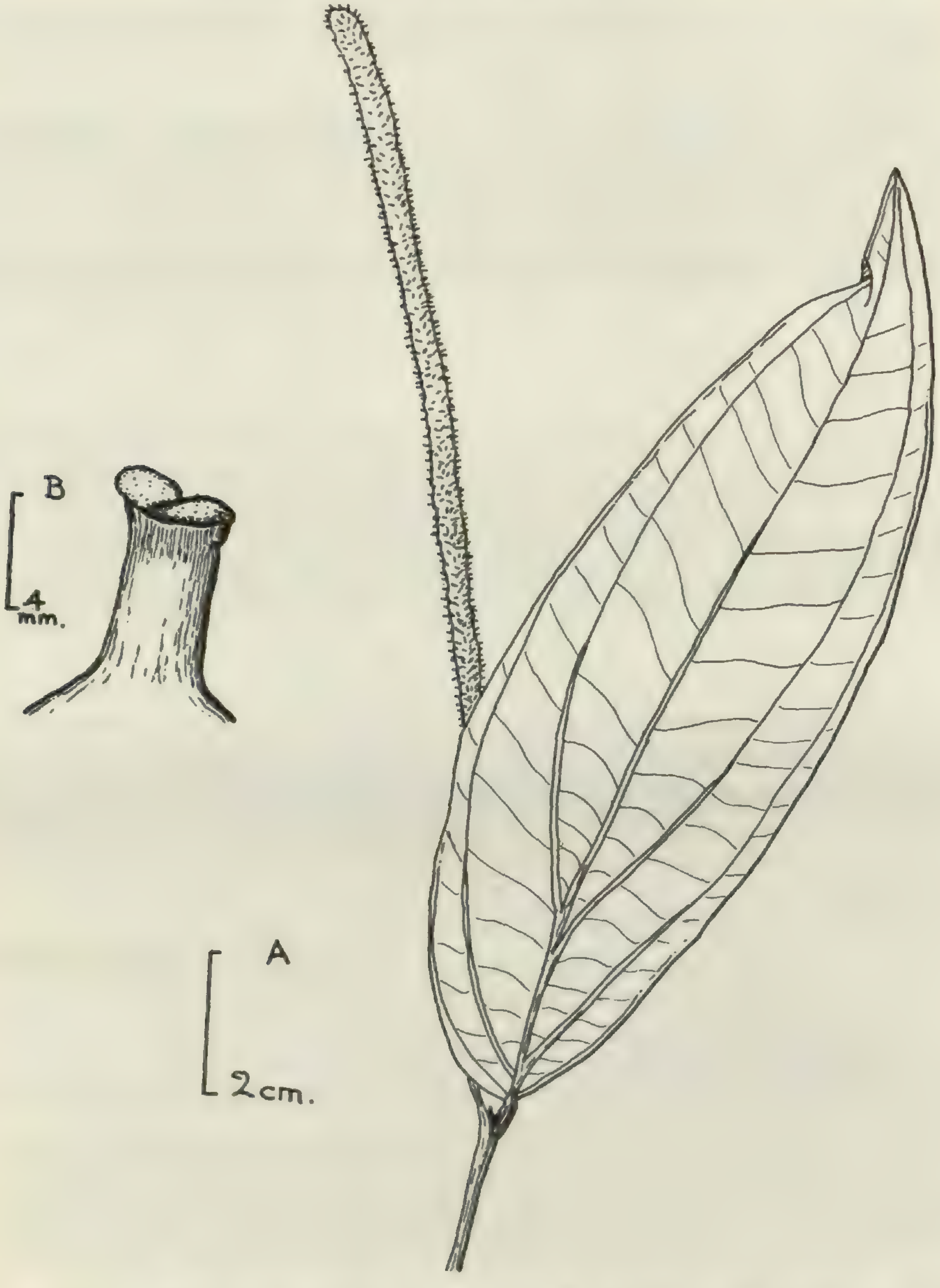

FIGURE 4. **Piper stenocarpum.** A, ♀ twig; B, stigma, from *Pullen 407*.

lipped, whereas in *P. mestonii* the inflorescences are shorter than the leaves, the peduncular stalks invariably of the same length as the petioles, and the stigmas very deeply 2-lipped.

The altitudinal range of our species extends from about 1500 to 3500 meters and overlaps that of *Piper mestonii* by about 500 meters at its lower limit. It has been reported to be commonest in fagaceous forests at about the 2200-meter contour.

The type collection was possibly gathered by George Belford who went

on an expedition to Mount Yule in Dec. 1890 and subsequently sent his material to Baron von Mueller in Melbourne.

14. **Piper versteegii** C.DC. Nova Guinea Bot. **8**(2): 415. 1910; Candollea **1**: 179. 1923.

P. rhizocaule Trelease, Jour. Arnold Arb. **9**: 149. 1928, *syn. nov.*

TYPE. West New Guinea. Noord-rivier; near Bivak-eiland: *Versteeg 1136*, March (lectotype in BO, L). FIGURE 5.

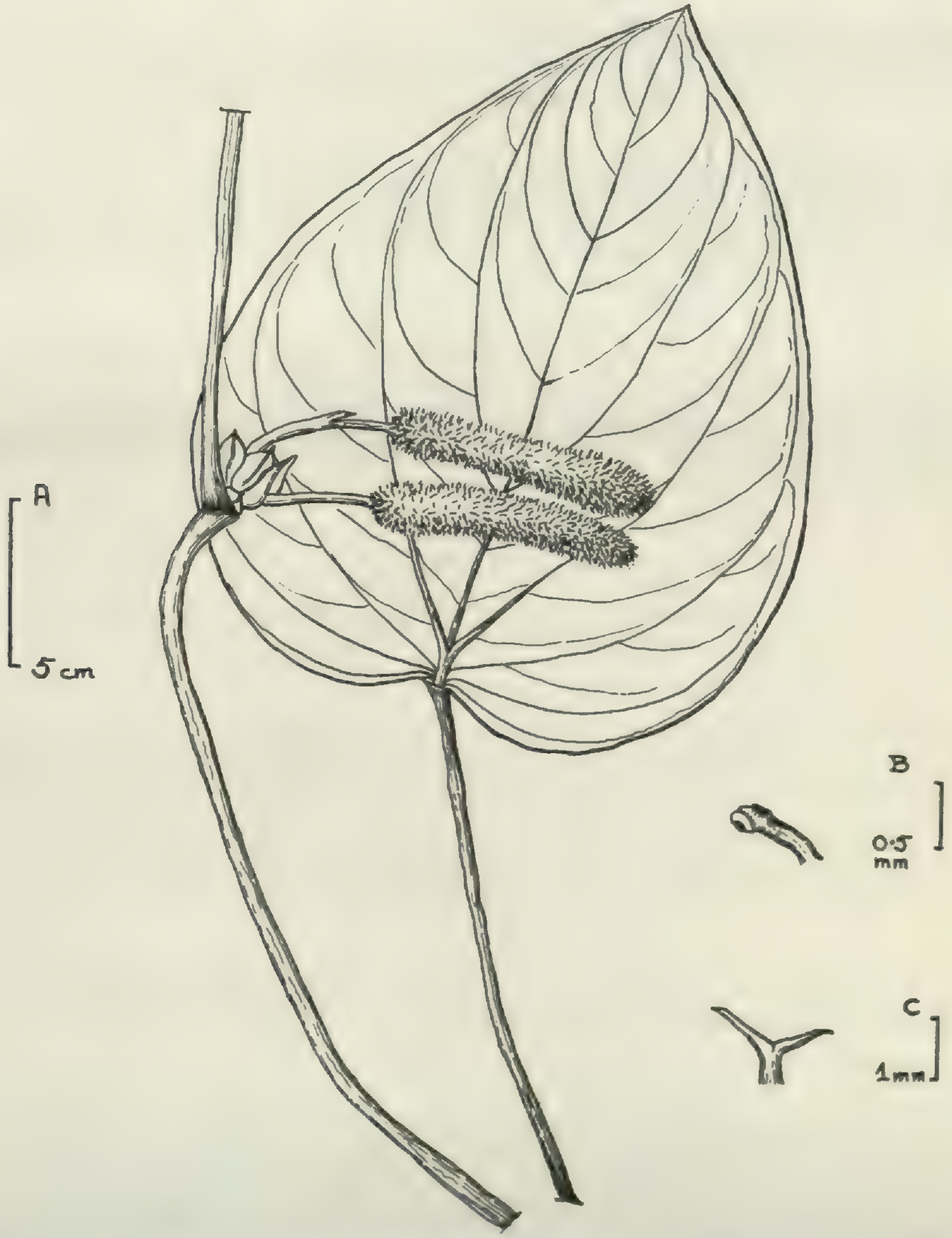

FIGURE 5. **Piper versteegii.** A, leaf and ♀ twig, from *Brass 14042*; B, stamen, from *van Royen NGF 16246*; C, stigma, from *Brass 14042*.

Dioecious climber, entirely glabrous. *Lamina* fairly long petiolate, ovate to very broadly ovate, ca. 25 cm. long, 18 cm. broad, length:breadth ratio 2:1 to 1:1; apex acuminate; base symmetrical, rounded to broadly cordate, often very slightly subpeltate; lateral veins 4–5 pairs, one pair arising ca. 1/5 up the midrib, the rest from the base, often another very short pair from the midrib near the apex. *Petioles* 12–15 cm. long, sheathing at the lower third. *Inflorescences* terminal, usually more than two at the end of side branches, the bases enclosed by bracts ca. 1.5 cm. long. *Male inflorescences* slender, to 14 cm. long; peduncles to 3 cm. long. *Female inflorescences* thicker, to 10 cm. long; peduncles ca. 2 cm. long. *Male flowers* 2-staminate; anthers oblong, 2-valved; filaments longer than anthers; bracts orbicular, shortly peltate. *Female flowers* sessile; stigmas 2-fid, rarely 3-fid, filiform, borne on short somewhat thick styles. *Fruits* ca. 2 mm. long, 1 mm. broad, oblong, partially concrescent at maturity.

DISTRIBUTION. New Guinea and Bismarck Archipelago.

West New Guinea. NORTHERN. Idenburg River: *Brass 14042*, April (BRI). SOUTHERN. Noord-rivier; near Bivak-eiland: *Versteeg 1136*, March (lectotype of *P. versteegii*, BO, L); Sabang: *Versteeg 1768*, Sept. (BO).

N.E. New Guinea. MOROBE DIST. Gurokar: *Brass 29399*, May (CANB, LAE); Rawlinson: *van Royen NGF 16246*, March (BRI, LAE, NSW); Wagau: *Millar NGF 23453*, June (LAE).

Papua. GULF DIV. Kira: *Brass 1115*, March (isotype of *P. rhizocaule*, BRI). NORTHERN DIV. Kokoda: *Carr 16313*, March (CANB). WESTERN DIV. Fly River: *Brass 7238*, July (BRI).

Bismarck Archipelago. NEW BRITAIN. Kandrian: *Sayers NGF 21973*, March (LAE, NSW).

I find no justification for maintaining in specific status Trelease's *Piper rhizocaule*. Having compared the type of *P. rhizocaule* with that of *P. versteegii*, I conclude that the two are entirely conspecific.

Piper versteegii bears a strong superficial resemblance to *P. mestonii*, particularly in the leaves; but on closer examination it is found to differ from the latter radically by the terminal inflorescences, more than two at each node and bracteate at the bases, by the broadly sheathing bases of petioles, the 2-fid stigmas, and the fruits only partially concrescent at maturity.

Because the inflorescences remain terminal at maturity, this species perhaps forms the link between section POTHOMORPHE which is characterized by axillary inflorescences and section PIPER in which the inflorescences are leaf-opposed.

15. **Piper wichmannii** C.DC. Nova Guinea Bot. **8**(2): 418. 1910.

P. erectum C.DC. Denkschr. K. Akad. Wiss. M.-N. Kl. Wien **89:** 528. *tab. 4, fig. 5b*. 1914, *syn. nov.*
P. schlechteri C.DC. Bot. Jahrb. **55:** 204. 1918, *syn. nov.*
P. arbuscula Trelease, Jour. Arnold Arb. **9:** 146. 1928, *syn. nov.*

TYPE. West New Guinea. Côte du Nord: *Atasrip 39*, Exped. Wichmann (BO, L).

FIGURE 6.

Dioecious shrubs. *Lamina* moderately petiolate; asymmetrically broad ovate; ca. 26 cm. long, 18 cm. broad, length:breadth ratio ca. 3:2; the upper side glabrous, the lower minutely hirtellous on the veins only; apex shortly acuminate; base asymmetrically deeply cordate; lateral veins 4 or 5 pairs, the distal pair arising from the midrib at ca. 1.5 cm. from the

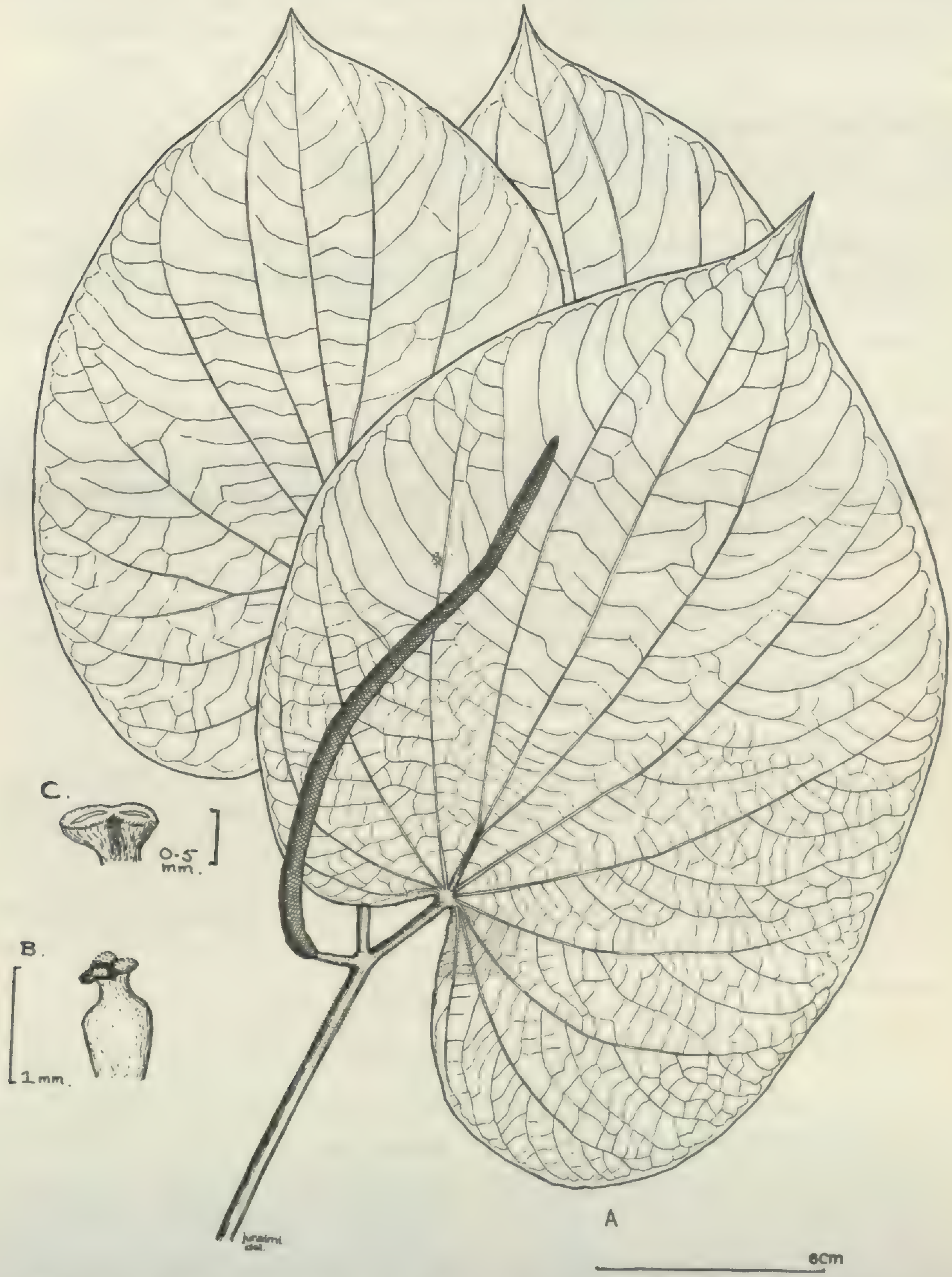

FIGURE 6. **Piper wichmannii.** A, ♀ twig; B, ovary; C, stamen. All from type.

base, the rest directly from the base, the broader side often with 1 or 2 more veins; margin ciliate. *Petiole* as long as the sinus of the base of the lamina is deep. *Stipules* ca. 5 cm. long, longer than petioles. *Inflorescences* up to as long as leaves, the females invariably shorter; peduncular stalks shorter than petioles. *Male flowers* 2-staminate; stamens 0.5 mm. long; anthers reniform, dehiscing apically; filaments short, broad, and stout. *Female flowers* sessile; stigmas 3-fid, subsessile; bracts round, peltate, long pedicellate. *Fruits* sessile, somewhat obconical, free at maturity.

DISTRIBUTION. New Guinea, Bismarck Archipelago, and Solomon Islands.

West New Guinea. WANDAMEN. Wondiwoi Mts.: *Schram BW 10742*, Feb. (LAE). VOGELKOP. Isjon River: *van Royen & Sleumer 7558*, Oct. (CANB, LAE). Sine loc.: côte du Nord: *Atasrip 39*, Exped. Wichmann (isotype of *P. wichmannii*, BO).

N.E. New Guinea. MOROBE DIST. Mt. Rawlinson: *Hoogland 9099*, June (BRI, LAE). SEPIK DIST. Djamu: *Schlechter 17584*, April (isotype of *P. schlechteri*, SING).

Papua. CENTRAL DIV. U-uma River: *Brass 1449*, May (isotype of *P. arbuscula*, BRI).

Bismarck Archipelago. NEW BRITAIN: *Floyd 3525*, Aug. (BO, BRI, CANB, LAE, NSW, SING); *Sayers NGF 24209*, March (CANB, LAE, NSW, SING).

Solomon Islands. BOUGAINVILLE. Kieta: *Kajewski 1538*, March (BO, BRI, SING); Kupei: *Kajewski 1725*, April (BRI). GUADALCANAL. Tutuve Mts.: *Kajewski 2601*, April (BO, BRI). SAN CRISTOBAL. Waimamura: *Brass 2589*, Aug. (BO, BRI, SING). SANTA YSABEL. Tiratona: *Brass 3319*, Dec. (BRI).

This is perhaps the commonest species of *Piper* in New Guinea and the Solomon Islands; and has been described as comprising handsome soft-wooded trees often with prop-roots. Its arborescent habit of growth coupled with the characteristically large cordate leaves with long spikes makes it the most distinctive species in the genus.

The three species listed in the synonymy above have been found to be entirely conspecific with *Piper wichmannii*. I have examined all the type materials (excepting *P. erectum*, of which I have seen an illustration) and I am confident that they are properly placed here.

The closest relative of this species is definitely *Piper grandispicum*, also of New Guinea, from which our species differs in having shorter inflorescences.

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The numbers in parentheses refer to the corresponding species in the text.

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Bloembergen *4615*, *4702* (3)
Boorsma *2* (3); *3* (9); *4* (4); *9* (6); *13* (9)
Boraule, *BSIP* nos. *9305* (15); *9478* (4)

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Cowmeadow, *BSIP* nos. *3281* (15); *3283*, *3782* (12); *4755* (15); *4762* (4); *4830* (8); *4836* (15); *4838* (12)
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Womersley et al., *NGF* nos. *6082, 6097* (7); *37258* (4)

ROYAL BOTANIC GARDENS
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AUSTRALIA

THE GENERA OF JUGLANDACEAE IN THE SOUTHEASTERN UNITED STATES [1]

THOMAS S. ELIAS

JUGLANDACEAE A. Richard ex Kunth, Ann. Sci. Nat. 2: 343. 1824, "Juglandeae," nom. cons.

(WALNUT FAMILY)

Trees [rarely shrubs] mainly of temperate regions, the branchlets terete, the wood durable, often dark-colored. Leaves deciduous [or evergreen], alternate [or opposite], petiolate, imparipinnate, usually glandular-dotted beneath and aromatic, exstipulate. Flowers imperfect. Staminate flowers borne in pendulous [rarely erect] aments, 3- to several-fasciculate on branches of the previous year or at the base of branches of the year, or solitary and lateral [or borne in a terminal cluster of several pendulous or erect aments with a central carpellate ament]; each staminate flower with a primary bract,[2] 2 secondary bracts [sometimes absent], and 4 or fewer perianth lobes, or the perianth sometimes absent (*Carya*, *Platycarya*); stamens 3–100, attached to the receptacle and borne in 1 to several series, the filaments short, free, the anthers basifixed, erect, 2-locular, with longitudinal dehiscence, a rudimentary gynoecium occasionally present. Carpellate flowers borne [on a central ament in a terminal cluster of staminate aments or] on a solitary [pendulous to] erect, often few-flowered spike, each sessile flower composed of a floral envelope and gynoecium, the floral envelope consisting of an involucre composed of a

[1] Prepared for a generic flora of the southeastern United States, a project of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of the National Science Foundation (Grant GB–6459X, principal investigator Carroll E. Wood, Jr.). This treatment follows the format established in the first paper of the series (Jour. Arnold Arb. **39**: 296–346. 1958). The area of the flora includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with additional information about extraterritorial taxa in brackets. References that I have not seen are marked by an asterisk.

I am grateful to Dr. Wood for his thorough editing, valuable suggestions in the course of this study, and the several weeks he devoted to the manuscript. Dr. Donald E. Stone has read the manuscript and has offered a number of useful and much-appreciated comments. Mrs. Nancy Dunkly has helped greatly in checking the bibliography and typing the manuscript. The illustrations are by Virginia Savage, largely from materials from the Arnold Arboretum supplemented by some preserved material of *Carya* kindly sent by Dr. Stone.

[2] The primary bract of *Alfaroa* and *Engelhardia* (*Engelhardtia*) is 3-lobed and is interpreted by Hjelmqvist (1948) as representing the fusion of two lateral secondary bracts with the primary bract.

primary bract [3-lobed in *Alfaroa* and *Engelhardia*] and 2 secondary bracts (occasionally modified or partly or wholly absent) and of a 4-parted perianth; primary and secondary bracts adnate at least to the base of the ovary, one or more perianth lobes occasionally modified or perianth absent (*Carya*); gynoecium syncarpous, usually of 2, rarely 3 or 4 carpels, the ovary inferior, 1-locular above, 2- or 4[8]-locular near the base, the single ovule erect, basal but at the apex of the incomplete septum(a), orthotropous, with a single integument; stigmas 2 (sometimes deeply 4-parted), sessile on the ovary, generally fleshy and papillate. Fruit drupaceous, a nut with a leathery or fibrous, dehiscent or indehiscent husk [3] [or fruit a nut with a wing or wings formed by the persistent primary and/or secondary bracts]; pericarp generally indurated, intrusive at the base, incompletely 2–4[8]-locular, the wall and septum(a) with or without longitudinal lacunae (cf. FIGURE 3, i, l). Seed large, filling the cavity of the pericarp, 2–4[8]-lobed; endosperm absent; seed coat thin; embryo oily, occasionally sweet, the large cotyledons variously lobed, twisted, or folded, the short radicle superior. Base chromosome number 16. TYPE GENUS: *Juglans* L.

A family of seven genera (eight if *Oreomunnea* Oersted is segregated from *Engelhardia* Leschen. ex Blume [4]), with approximately 60–65 species distributed primarily in temperate regions of the Northern Hemisphere but extending southward in montane areas of tropical America and Asia. The family is not known to be represented in either Africa or Australia, although *Engelhardia* reaches Java and New Guinea. *Platycarya* Sieb. & Zucc., *Pterocarya* Kunth, and *Cyclocarya* Iljinsk., are restricted to the Old World, *Alfaroa* Standl., is confined to the New, and *Engelhardia*, *Carya* Nutt., and *Juglans* L. are represented in both hemispheres (but see footnote 4). *Carya* and *Juglans* represent the family in the southeastern United States.

The family Juglandaceae is considered by Lawrence (1951) to comprise the monotypic order Juglandales, while Takhtajan (1969) includes the monotypic Rhoipteleaceae on the basis of the pinnately compound leaves and hard wood of *Rhoiptelea*, and Stone & Broome have found that the pollen ultrastructure of Juglandaceae and Rhoipteleaceae is compatible. Hutchinson (1967) and Cronquist (1968) include both families and the trifoliolate-leaved Picrodendraceae in the Juglandales. This order is closely allied with the Myricales, Betulales, and Fagales. The Juglandaceae are distinguished from other Juglandales by the unisexual flowers borne in catkins; the drupaceous or nut-like fruit; the solitary basal,

[3] The husk (incorrectly called "exocarp" by some authors) is derived from the involucre and the perianth, while the hard shell of the nut is derived from ovarian wall that becomes sclerified before maturity.

[4] Although *Oreomunnea* has traditionally been considered to be congeneric with *Engelhardia*, Stone (Ann. Missouri Bot. Gard., in press) has reëxamined the evidence and thinks that the two should be recognized as distinct genera. *Engelhardia* as then circumscribed is restricted to the Old World, *Oreomunnea* to the New.

orthotropous ovule with a single integument borne in a 1-locular, inferior ovary; and the pinnately compound, exstipulate leaves.

Pollen studies by Whitehead (1965) have shown that the family includes several types. On the basis of ten characters that presumably indicate evolutionary trends within the family (including increase in size, sphericity, presence of pseudocolpi, distinctness of the columellae, irregular thickening of the ektexine, increase in pore number, increase in heteropolarity, and various ektexinous thickenings) *Engelhardia Roxburghiana* Wall. is considered to have the least specialized pollen. Pollen of *Engelhardia* and of the somewhat more specialized *Alfaroa* is isopolar and triporate (occasionally tetraporate, rarely pentaporate). Pollen of *Platycarya* is also basically triporate (bi- to pentaporate) but the presence of arcuate pseudocolpi indicates increased specialization. Distinctly larger and definitely heteropolar, the pollen grains of *Carya* are generally triporate. The specialized grains found in *Juglans* and *Pterocarya* are large, stephanoporate to basically periporate, and heteropolar. In *Juglans* the pores may vary from 2 to 37 per grain, with 6 to 18 the prevailing numbers. According to Erdtman, the Juglandaceae have several pollen characters in common with the Betulaceae, Casuarinaceae, Myricaceae, and Rhoipteleaceae.

Studies of the secondary xylem have shown that of *Alfaroa* and *Engelhardia* to be the least specialized (Heimsch & Wetmore, 1939). The diffusely distributed vessels of *Alfaroa* have thin walls and the vessel elements have scalariform perforations. Although similar, the wood of *Engelhardia* appears to be more specialized in its ring porosity. *Juglans* and *Pterocarya* are closely allied in several common anatomical features, although *Juglans* appears to be slightly more specialized. Anatomically *Platycarya* is somewhat isolated, having attained a high degree of specialization in the inflorescence, while the wood is relatively unspecialized as in *Alfaroa* and *Engelhardia*. The greatest specialization in the secondary xylem, i.e., distinct ring porosity and rounded, thick-walled vessels, has been reached by *Carya*. Iljinskaya (1953) notes that *Cyclocarya* has ring-porous wood as in *Carya* and *Platycarya*. Since *Alfaroa* and *Engelhardia* exhibit less specialized wood structure than the Anacardiaceae, it seems improbable that the Juglandaceae were derived from the Anacardiaceae as suggested by Cronquist (1968).

From a morphological study of the inflorescences and flowers of the Juglandaceae, Manning (1938, 1941, 1948) concluded that *Carya* and *Juglans* are the most specialized and *Engelhardia* and *Alfaroa* the least specialized genera of the family. Evolutionary trends leading to the Juglandaceae apparently included the development of imperfect-flowered axillary catkins from a terminal, highly branched panicle of perfect flowers. In general, the reduction of floral parts in the Juglandaceae supports the conclusions drawn from pollen and anatomical studies.

Various authors have grouped the genera of Juglandaceae into two subfamilies on the basis of the fruit type (winged, nutlike fruits *vs.* unwinged, drupaceous ones), but this distinction appears to be an artificial one.

In addition, there also appears to be no validly published name available for the subfamily that does not include *Juglans* when such a division is made. The names Nuciferoideae and Drupoideae proposed by Koidzumi (Acta Phytotax. Geobot. 6: 10. 1937) are not based on those of genera; Oreomunnoideae Leroy (Mém. Mus. Hist. Nat. Paris Bot. II. 6: 86. 1955) was published without a Latin description and indication of the type; and the properly formed name Pterocaryoideae used by Melchior (A. Engler's Syllab. Pflanzenfam. ed. 12. 2: 42. 1964) in place of Nuciferoideae is also invalid since he neither gave a full and direct reference to Koidzumi's description (as required by ICBN, Art. 33) nor supplied a Latin description and a type.

The extant genera and species of Juglandaceae appear to be the remaining stocks of a once large and much more widespread family. If identifications of fossils are correct, the earliest records of Juglans are from the Middle to Upper Cretaceous. *Carya* has not been attributed to the Cretaceous, although it was abundant in the Tertiary and present in later times. Fossils of *Engelhardia* and *Platycarya* are also known, and several extinct genera have been described.

The Juglandaceae are of considerable economic importance for their excellent wood and nuts (*Juglans*, *Carya*, *q.v.*). Several species of *Pterocarya* and the handsome shrubby tree *Platycarya strobilacea* Sieb. & Zucc. are cultivated as ornamentals in the United States.

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KEY TO THE GENERA OF JUGLANDACEAE IN THE SOUTHEASTERN UNITED STATES

General characters: *trees with hard, dark-colored wood; leaves pinnately compound, exstipulate; leaflets usually glandular-dotted beneath; flowers imperfect, the plants monoecious; staminate flowers bracteate, in pendulous aments, with or without a perianth; carpellate flowers bracteate, solitary or in small clusters, or in few-flowered spikes; perianth present (sometimes modified) or absent; gynoecium bicarpellate, ovary 1-locular, the single orthotropous ovule erect, basal; fruit drupaceous with a slightly fleshy or fibrous dehiscent or indehiscent husk surrounding a one-seeded nut; seed large, bilobate, germination hypogeal.*

Branchlets with continuous pith; leaflets with involute vernation; staminate aments usually 3-fascicled; stamens to 8 or 10 per flower (usually 4); perianth absent; carpellate flowers without a perianth; fruit dehiscent or partially dehiscent, husk usually splitting into 4 valves, the nut usually smooth. ..... 1. *Carya.*

Branchlets with chambered pith; leaflets with conduplicate vernation; staminate aments solitary or in pairs, stamens to 40 per flower; perianth 3–6-lobed; carpellate flowers with a 4-lobed perianth; fruit with an indehiscent husk, the nut irregularly furrowed. ..... 2. *Juglans.*

1. **Carya** Nuttall, Gen. N. Am. Pl. **2**: 220. 1818, nom. cons.

Trees of varied woodland habitats, with smooth or exfoliating, aromatic, resinous, gray bark; heartwood hard, brown, sapwood pale; branchlets terete, tough, flexible, with continuous pith, the bud scales few and valvate or numerous and imbricate, the axillary buds[5] smaller than the terminal bud. Leaves few- to many-foliolate, often glandular dotted beneath, petiolate, leaf scar large, elevated, oblong or semiorbicular, often 3-lobed, emarginate; leaflets involute in vernation, usually ovate to obovate, generally acuminate at apex, mostly oblique at base, serrate [entire],

[5] Paired valvate prophylls, probably protective in function, completely inclose (except for a terminal pore) the inner portions of the axillary buds.

FIGURE 1. **Carya** section **Apocarya.** a–h, *C. cordiformis*: a, staminate flower, × 12; b, stamen, × 15; c, three-lobed primary bract subtending stamens, × 10; d, branchlet with two carpellate flowers, × 1 1/2; e, carpellate flower and involucre, × 8; f, mature fruit with involucre dehiscing — note winged margins of valves, × 1; g, mature nut, × 1; h, terminal branchlet in winter condition with lower part in longitudinal section to show homogeneous pith, × 1. i–l, *C. illinoënsis*: i, mature fruit with involucre, × 1; j, mature fruit with one involucral valve removed, × 1; k, seed, × 1; l, terminal branchlet, winter condition, × 1. m, n, *C. myristiciformis*: m, mature fruit with involucre dehiscing, × 1; n, mature nut, × 1. o, *C. aquatica*: mature fruit with one involucral valve removed.

often subcoriaceous, sessile to short-petiolulate, becoming bright yellow in the fall. Flowers vernal, usually appearing after leaves unfold. Staminate flowers borne in slender, pendulous aments, these occurring singly or 5–8 in fascicles in the axils of the leaves of the previous year (occasionally of the current year) or at the base of the inner scales of the terminal bud; each flower subtended by a persistent, lanceolate bract; perianth absent, the floral envelope usually 2(3)-lobed, consisting of one primary plus two secondary bracts, the primary one linear to lanceolate, free to

near the base and usually much longer than secondary bracts, secondary bracts ovate, rounded to acuminate at the apex, fused with the primary bract near the base; stamens 3–10(–15), 2- or 3-seriate, inserted on the slightly thickened receptacle-like inner and lower face of the floral envelope; the anthers ovate-oblong, emarginate or divided at the apex, yellow or red, generally pilose or hirsute, as long as or longer than their slender connectives, the filaments abbreviated, free; gynoecium absent. Carpellate flowers borne in 2–10-flowered spikes terminal on branches of the year; perianth absent, each flower surrounded by a 4-lobed slightly 4-ridged involucre that is villose and covered on the outer surface with yellow glandular scales that ± persist in fruit; involucre often unequally lobed, composed of a primary bract and a 3-lobed structure probably representing 3 secondary bracts. Gynoecium bicarpellate, 4-locular at base, 2- and then 1-locular above at level of ovule (cf. FIGURE 2, f–h); stigmas spreading, papillate, ± united at the base, often persistent. Fruit often ovoid, globose or pyriform, the involucre of varying thickness, becoming indurated at maturity, 4-valved, promptly or tardily dehiscent to the middle or to the base; nut usually oblong, obovate or subglobose, narrowed and usually rounded at base, with 2 abaxial sutures, each valve enclosing half of each cotyledon, usually smooth externally, variously ridged internally, 4-locular at the base, above becoming 2-locular (by an incomplete middle septum separating the basal parts of cotyledons) and then 1-locular. Seed usually filling the nut cavity; testa thin, membranaceous; embryo with large fleshy cotyledons, the cotyledons oily, sweet to bitter, 2-lobed to near midway, the lobes oblong, compressed, with various longitudinal grooves, ± concave on the inner surface; radicle short, superior. Base chromosome number 16. (*Hicorius* Raf., 1817, nom. rejic.; *Hicoria* Raf., 1838, orth. mut.; *Pecania* Dochnahl.) LECTOTYPE SPECIES: *C. tomentosa* (Poiret) Nutt. (*Juglans tomentosa* Poiret), *typ. cons.* (Ancient Greek name, *karya*, applied to *Juglans regia*.) — HICKORY.

A genus of 15 species mainly of temperate eastern North America and southeastern Asia, represented in the eastern United States and parts of adjoining Mexico by 11 species, absent from western North America, although present there during the Tertiary. Four species occur disjunctly in southeastern Asia. The determination of the species of *Carya* should be approached with caution, for in addition to occasional hybrids, considerable intraspecific variation has lead to the description of numerous varieties, most of which are without merit. Although fruiting collections are often necessary for accurate identification, careful floral analysis should yield valuable data for distinguishing the species and understanding their biology.

Section APOCARYA C. DC. (*Hicorius* subg. *Pacania* Raf., subg. *Drimocarya* Raf.; *Hicorius* § *Apohicoria* Dippel; *Carya* § *Pacania* (Raf.) Rehder) contains eight species disjunctly distributed between the eastern United States, Mexico, and Asia. The species comprising this section have 5–17 serrate, usually falcate leaflets, 4–6 valvate bud scales (buds pos-

sibly naked in *C. cathayensis*) that are hardly or not at all accrescent in spring, 3–8 (usually 4) stamens, a husk with the valves not keeled but frequently narrowly winged along the margins, and lacunose wall partitions in the nut. At least all of the American species of the section are diploids, $2n = 32$, whereas species of section CARYA are predominantly tetraploid (Stone, 1963).

Four species of sect. APOCARYA are found in the southeastern United States. An important component of the deciduous forest of the eastern United States, *Carya cordiformis* (Wangenh.) K. Koch, bitternut hickory, $2n = 32$, occurs from New Hampshire, southernmost Quebec, New York, and southern Ontario, west to Minnesota and southeastern Nebraska, and south to northwestern Florida, eastern Oklahoma, and eastern Texas (see Little, 1971, *map 112-E*). This species is characterized by scurfy-yellow overwintering buds, lanceolate to lanceolate-ovate, scarcely falcate leaflets that are pubescent beneath, and cylindric to compressed fruit with the valves of the husk narrowly four-winged above the middle. It occurs most commonly in moist sites and reaches its greatest height (over 30 m.) in the rich bottomlands of the lower Ohio River basin. Hybrids with *C. illinoënsis* (*C.* × *Brownii* Sarg.), *C. glabra* (*C.* × *Demareei* Palmer), and *C. ovata* (*C.* × *Laneyi* Sarg.) have been reported.

The bitternut hickory is allied to *Carya Palmeri* Manning, an endemic of Nuevo León, Tamaulipas, and San Luis Potosí, Mexico, that differs from *C. cordiformis* in having tight, smooth bark, in the 11 (9–13) occasionally falcate leaflets, in the more frequently hairy rachises and twigs, and in the glandular peltate scales on the undersurface of the leaflets. On the basis of similarities in leaf margins, stomata, trichomes, bracts protecting the axillary buds, and fruit, Stone (1962) demonstrated close relationships between *C. cordiformis* and *C. Palmeri* and the Asian *C. tonkinensis* and *C. cathayensis*. Stomatal guard-cell size indicates that *C. Palmeri* is a diploid (Stone, 1961).

Abundant only in Arkansas on high bottom-flats of the Mississippi River Delta, *Carya myristiciformis* (Michx. f.) Nutt. (*C. "myristicaeformis,"* orth. error), nutmeg hickory, $2n = 32$, is also found sparingly in scattered localities in eastern South Carolina, Alabama, and Mississippi, and in southeastern Oklahoma, Louisiana, and eastern Texas, as well as disjunctly in Nuevo León and Tamaulipas, Mexico (see Little, 1971, *map 116-E*). Often a tall tree (to ca. 35 m.), *C. myristiciformis* has a nut with a thick hard shell; ovate-lanceolate to broadly obovate, more or less falcate leaflets; and long-pedunculate staminate catkins borne at the base of branchlets of the year. This species is not known to form hybrids.

Largely restricted to bottomlands and swamps, *Carya aquatica* (Michx. f.) Nutt. (*Hicorius aquaticus* (Michx. f.) Britton), water hickory or bitter hickory, $2n = 32$, is found primarily on the Coastal Plain from southeastern Virginia and eastern North Carolina to southern Florida and eastern Texas, and in the Mississippi Embayment to southeastern Oklahoma, western Tennessee, southeastern Missouri and southern Illinois (see Little, 1971, *map 111-E*). The distinctive characters of this species include the

exfoliating bark, the reddish-brown, yellow-glandular overwintering buds, the lanceolate-falcate leaflets, and the laterally compressed nut with husk wings extending to the base. *Carya aquatica* is reported to hybridize with *C. texana* (*C.* × *ludoviciana* (Ashe) Little) and with *C. illinoënsis* (*C.* × *Lecontei* Little). In a study on the hybridity of *C.* × *Lecontei* by an examination of the fatty acids in the oil of the embryo, Stone, Adrouny & Adrouny found that the reputed hybrid contained amounts of fatty acids intermediate with the two probable parents.

The pecan, *Carya illinoënsis*[6] (Wangenh.) K. Koch (*C. olivaeformis* (Michx.) Nutt., *C. Pecan* (Marsh.) Engl. & Graebn., *Hicorius Pecan* (Marsh.) Britton), appears to be native to the Mississippi River Valley from southern Indiana, northern Illinois, and southeastern Iowa, to Alabama, Mississippi, Louisiana, and eastern Texas, but its original range is difficult to determine since it probably was spread by Indians, and it has been widely planted throughout most of the southeastern United States. It also occurs in scattered localities from Coahuila and Nuevo León, Mexico, southward to Jalisco, Hidalgo, and Oaxaca (see Little, 1971, *maps 114-W, 114-E, 114-N*). The combination of overwintering buds covered with clusters of yellow hairs; oblong-lanceolate leaflets, the lower pairs falcate; staminate catkins sessile or subsessile near the summit of shoots of the preceding year; and elongate fruits distinguishes the species. In addition to hybrids with *C. cordiformis* and *C. aquatica*, *C. illinoënsis* is reported to hybridize with *C. laciniosa* (*C.* × *Nussbaumeri* Sarg.) and with *C. tomentosa* (*C.* × *Schneckii* Sarg.), of sect. CARYA.

The remaining species of sect. APOCARYA are Asiatic. *Carya cathayensis* Sarg. has been reported from Chekiang, Kweichow, and Kiangsi provinces, China. The closely related *C. tonkinensis* Lecomte has been collected in Yunnan, China; Tonkin, North Viet Nam; and Assam, India. *Carya Poilanei* (A. Chev.) Leroy is also known from Tonkin and from Laos. The only other Asiatic species of *Carya*, *C. sinensis* Dode, has been segregated from sect. APOCARYA to form the monotypic sect. RHAMPHOCARYA Manning & Hjelmqvist (*Annamocarya* A. Chev.), mainly on the basis of its 7–9 entire leaflets, either hollow or solid pith, few and unequal bud scales, staminate catkins in fascicles of five to eight, 5–15 stamens, 4–6 apically keeled valves of the husk, and lacunae absent in the lower part of the walls of the nut but sometimes present near the apex.

The New World section CARYA (*Carya* § *Eucarya* C. DC.; *Hicorius* subgen. *Glycaria* Raf., subgen. *Hexacarya* Raf.; *Hicorius* § *Euhicorius* Dippel, § *Eucarya* (C. DC.) Sarg.) contains seven species of the eastern United States and northeastern Mexico. Species of this section have 3–9 serrate, nonfalcate leaflets; 6–12 imbricate bud scales that are strongly accrescent in spring; 3–8, but usually 4, stamens; a 4-valved husk with the valves neither strongly keeled nor winged along the margin; and wall

[6] According to Thieret (1961) the original, and consequently correct, spelling of the epithet is *illinoinensis*. The Standing Committee on Stabilization appointed by the XI International Botanical Congress (1969) has ruled, however, that *illinoinensis* is an orthographic error and the spelling *illinoënsis* should be retained.

FIGURE 2. **Carya** section **Carya.** a–m, *C. ovata* var. *australis*: a, flowering branchlet with staminate and carpellate inflorescences, × 1/3; b, staminate flower, × 10; c, stamen, × 12; d, bracts subtending staminate flower, × 10; e, carpellate flower, × 6; f, semidiagrammatic longitudinal section of carpellate flower showing ovule, × 6; g, semidiagrammatic basal cross section of carpellate flower (at level of lower arrow in "f"), showing four-loculate condition of

partitions of the nut without lacunae. All the species of this section that have been examined are tetraploid, $2n = 64$, with the exception of the diploid *C. laciniosa* and *C. ovata*.

Common in rich woods, bottomlands, and on slopes, *Carya ovata* (Mill.) K. Koch (*Hicorius ovatus* (Mill.) Britt.), $2n = 32$, shagbark hickory, is found throughout most of the eastern United States from southeastern Nebraska and southeastern Minnesota to southern Maine, southward to Georgia, Alabama, Mississippi, Louisiana, and eastern Texas, and disjunctly in Mexico (Tamaulipas and Nuevo León south to Hidalgo and Puebla). It is largely absent from the southeastern Coastal Plain (see Little, 1971, *maps 118-N, 118-E*). Little (1969) recognizes two varieties: var. *ovata* (including *C. mexicana* Engelm. ex Hemsl.) and var. *australis* (Ashe) Little (*C. carolinae-septentrionalis* (Ashe) Engl. & Graebner, *C. australis* Ashe), Carolina hickory or southern shagbark hickory. Several varieties described by Sargent do not appear to be worthy of recognition. The fruits usually longer than 3.5 cm., the dark brown or black terminal bud scales, and the generally lanceolate or oblanceolate terminal leaflets of var. *australis* serve to separate it from var. *ovata* with its smaller fruits (less than 3.5 cm. long), tan or light brown bud scales, and usually obovate terminal leaflets. *Carya ovata* is reported to hybridize with *C. laciniosa* (*C.* × *Dunbarii* Sarg.) and *C. cordiformis* (*C.* × *Laneyi* Sarg.).

The other diploid member of sect. CARYA, *C. laciniosa* (Michx. f.) Loudon (*Hicorius laciniosus* (Michx. f.) Sarg.), shellbark hickory, $2n = 32$, is common in rich woods and bottomlands, mainly in the Ohio and Mississippi valleys. It reaches the northern limit of its range in western New York and southern Ontario and extends westward to southern Iowa and Missouri, and southward to West Virginia, Kentucky, Tennessee, Arkansas, and northeastern Oklahoma, with local occurrences in Virginia, North Carolina, Georgia, Alabama, and Mississippi (see Little, 1971, *map 115-E*). It is closely related to *C. ovata* but is distinguished from it by orange-brown or light tan branchlets; by the larger bud scales, glabrous above and accrescent; by oblong-lanceolate to oblong-obovate acuminate leaflets that are soft-pubescent beneath and lack the prominent tufts of hairs located on the serrate margins of leaves of *C. ovata*; and by a large, angled, more or less strongly compressed nut with a yellowish- to reddish-brown shell. Hybrids of this species with *C. ovata* (*C.* × *Dunbarii* Sarg.) and with *C. illinoënsis* (*C.* × *Nussbaumeri* Sarg.) have been reported.

Carya pallida (Ashe) Engl. & Graebn. (*Hicorius pallidus* Ashe), sand

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ovary, × 8; h, semidiagrammatic median cross section of carpellate flower (at level of upper arrow in "f"), showing ovule filling the single locule at this level, × 8; i, mature fruit with involucre beginning to split, × 3/4; j, mature fruit with two involucral lobes removed, × 3/4; k, nut, × 3/4; l, median cross section of nut — cotyledons of embryo white, sclerified wall of nut hatched, × 3/4; m, terminal bud, winter condition, × 1. n–s, *C. laciniosa*: n, staminate flower, × 10; o, stamen, × 12; p, bracts subtending staminate flower, × 10; q, carpellate flower, × 6; r, terminal bud, winter condition, × 1; s, young seedling, × 1/6.

hickory, is largely confined to the Coastal Plain from southern New Jersey to northwestern Florida and Louisiana, and north in the Mississippi Embayment to Tennessee and southeastern Kentucky. Deam (1940) reported it from Knox County, Indiana. It is readily distinguished by the combination of silvery-lepidote overwintering buds and staminate inflorescences; long-attenuate resinous and aromatic leaflets that are silvery-lepidote beneath when expanding; and yellow-lepidote husk that tardily splits to the base (Fernald, 1950). The chromosome number of *C. pallida* has not been determined, but on the basis of stomatal guard-cell size it is presumed to be tetraploid (cf. Stone, 1961). No hybrids with other species have been reported.

Common in most of the eastern United States, generally in dry woods and on slopes, *Carya glabra* (Mill.) Sweet (*Hicorius glabrus* (Mill.) Britt.; *C. leiodermis* Sarg., cf. Little, 1969), $2n = 64$, is characterized by close, usually furrowed and rigid bark; acute overwintering terminal buds that are glabrous at first but become silky pubescent in autumn; glabrous petioles, rachis, and leaflets; and obovoid, dark brown, smooth, shining fruit with the husk indehiscent or opening tardily by only one or two sutures. Little (1969) recognized two varieties in this species in addition to var. *glabra* (*C. microcarpa* Nutt., *H. microcarpus* (Nutt.) Britt.), which occurs from Massachusetts and southern New Hampshire to New York, southern Ontario, southern Michigan, Illinois, and northeastern Kansas, south to Arkansas, Mississippi, Georgia and northwestern Florida. Varietas *megacarpa* (Sarg.) Sarg. (*C. Ashei* (Sudw.) Kelsey & Dayton, *H. austrinus* Small, *C. austrina* (Small) Murrill), coast pignut hickory, with larger leaflets and fruits, is found from western New York to southern Ohio and Illinois, south to eastern Texas, Louisiana, and central Florida. Varietas *odorata* (Marsh.) Little (*C. ovalis* (Wangenh.) Sarg., *C. ovalis* var. *odorata* (Marsh.) Sarg.), red hickory, with a smaller globose or pyriform fruit, the husk of which splits to the base by four sutures, is of scattered occurrence throughout most of the range of var. *glabra*. (See Little, 1971, *map 113-E*, for distribution of the species.)

A small tree or shrub confined to the scrub of dry sand-ridges from central to northwestern Florida, *Carya floridana* Sarg. (*Hicorius floridanus* (Sarg.) Small), Florida or scrub hickory, $2n = 64$, is closely related to *C. glabra*, which in Florida occurs largely in hammocks, and to *C. texana*, which has a similar rusty pubescence of undulating peltate scales on the young leaves. Kurz & Godfrey (1962) question the taxonomic distinctness of *C. floridana*, since intergrades with *C. glabra* can be found in intermediate habitats. *Carya floridana* is separated from *C. glabra* largely by its habitat and by the characteristic rusty pubescence of the young leaves.

Carya texana Buckl. (*C. Buckleyi* Durand, *C. villosa* (Sarg.) Schneider, *C. arkansana* Sarg.), black hickory, $2n = 64$, occurs from eastern Kansas, Missouri, southern Illinois, and southern Indiana to eastern Oklahoma, central Texas, and southern Louisiana. Related to both *C. ovata* and *C. floridana*, *C. texana* typically has rusty-pubescent young branchlets and overwintering buds, bud scales hairy-tufted at the apex, leaflets rusty-

pubescent beneath with peltate scales, and yellow-scurfy fruit with the husk splitting either to the middle or nearly to the base. This species appears to be restricted to dry upland woods or dry sandy or rocky slopes. A hybrid between *C. texana* and the bottomland diploid *C. aquatica* (*C.* × *ludoviciana* (Ashe) Little) has been reported, but according to Little (1953) additional study is needed to determine its true identity. Laughlin has described a hybrid between *C. texana* and *C. tomentosa* (*C.* × *collina* Laughlin).

A woodland species, *Carya tomentosa* (Poiret) Nutt. (*C. alba* (Mill.) K. Koch non (L.) Nutt. ex Ell., nom. ambig.), mockernut hickory, $2n = 64$, is found from New Hampshire, southernmost Ontario, southern Michigan, and southeastern Iowa, south to northern Florida and eastern Texas (see Little, 1971, *map 117-E*). *Carya tomentosa* is separated from the phenotypically similar *C. laciniosa* and *C. ovata* by its tomentose branchlets, petioles, rachises, and lower leaf surfaces, with the trichomes usually being curly and fasciculate; by the outer bud scales deciduous in autumn, thus exposing the inner silky scales; by a husk that splits to or below the middle; and by the deeply furrowed but not exfoliating bark. In Illinois and Iowa it is known to hybridize with *C. illinoënsis* (*C.* × *Schneckii* Sarg.).

Most speculations about phylogenetic relationships within *Carya* have had to rely on morphological observations, but an analysis of the oils from the seeds of the different species has provided some additional insights into interspecific alliances. Stone, Adrouny & Adrouny (1969) found oils from members of sect. APOCARYA to have high oleic and low linoleic content, while species of sect. CARYA have a low ratio of oleic to linoleic acid. Ties between the two sections are found in the average oleic and linoleic acid values of *C. myristiciformis* and *C. aquatica*, of sect. APOCARYA, and *C. ovata* var. *australis* (*C. carolinae-septentrionalis*) and *C. laciniosa*, both diploids of sect. CARYA. Oil data also link *C. ovalis* with *C. aquatica*, *C. myristiciformis*, *C. laciniosa*, and *C. ovata*, although *C. ovalis* has traditionally been considered allied to *C. glabra*, and Little recently (1969) reduced *C. ovalis* to a variety (*odorata*) of *C. glabra*. The data support the close assemblage of *C. floridana*, *C. texana*, *C. tomentosa*, *C. pallida*, and *C. glabra*, and within this group of tetraploids, *C. floridana* and *C. texana* appear to be closely allied. A somewhat distant relationship was established between *C. illinoënsis* and *C. cordiformis*. Although it was impossible to test the oils from any of the Asiatic species, it was suggested that ties with them might be via *C. myristiciformis* and *C. aquatica*.

A perianth is considered by morphologists to be lacking in carpellate flowers of *Carya*, and the four structures surrounding the gynoecium are considered to represent involucral bracts. Manning (1941) has designated the lower or united basal part of the two stigmas as a "stigmatic disk," which represents a modified calyx, but he has not published supporting anatomical evidence. Developmental and detailed anatomical studies should be helpful in determining the nature of the accessory structures of the carpellate flowers.

Flowering of *Carya* species occurs in the spring (usually in April and May) with the enormous amounts of pollen being dispersed by wind. In a study of commercial cultivars of *C. illinoënsis*, J. G. Woodroof (1930) found that 26 were proterandrous, 18 proterogynous, and 88 homogamous. Warm, sunny days were found to be optimal for pollen shedding, high humidity or rain retarding or completely stopping anther dehiscence. In *C. illinoënsis* the Polygonum-type embryo sac is at the four-celled stage at the time of pollination. Fertilization apparently does not occur for five to seven weeks following pollination, although Shuhart (1932) reported only a two-week lag. Embryogeny in *C. glabra* is of the Asterad type.

Pollination studies of *Carya illinoënsis* have shown it to be capable of both self- and cross-pollination. Following self-pollination, however, a greater number of immature nuts are dropped, resulting in smaller yields of harvested nuts than from the cross-pollinated trees. The staminate inflorescences are differentiated during the summer and mature the following spring, while carpellate inflorescences apparently do not differentiate until late winter or early spring. Throughout much of the south-central United States, *C. illinoënsis*, a prodigious pollen producer, is a major factor in many spring pollen allergies.

The pollen grains of *Carya* are tectate, usually triporate, suboblate, rounded-triangular to circular in polar view, with finely scabrate sculpturing. They are distinctly heteropolar, the pores being slightly off the equator of the grain and the aperture $\pm$ circular in outline (Whitehead, 1965). It appears from pollen morphological relationships that sect. CARYA is derived from sect. APOCARYA. Stone (1963) pointed out that most species belonging to sect. APOCARYA (all diploids) have pollen grains smaller than 46 μ, while species of sect. CARYA (mainly tetraploids) have pollen grains larger than 46 μ. There is also a positive correlation between stomatal size and ploidy level.

Species of *Carya* were widespread (pantemperate?) during favorable climates of the Tertiary. Fossils of *Carya* of Eocene and Miocene age are known from Alaska, the western and northwestern United States, Vermont, the southeastern United States, Greenland, Iceland, Spitzbergen, Central Europe, Russia (Kamchatka), and China (Shantung). There are apparently no good Cretaceous records.

Several species of *Carya* (*C. ovata*, *C. laciniosa*, *C. tomentosa*, and *C. glabra*) are the main sources of hickory lumber. The seeds of most species of *Carya* are high in tannins and consequently are not used as a food source, although they are an important food for wildlife. Nuts produced by *Carya ovata* and *C. laciniosa* are reported to be sweet, edible, and of good quality. The pecan, obtained from *C. illinoënsis*, has become one of the world's important nut crops. Interest in commercial pecan growing, largely in the early 1900's, has resulted in the description of numerous horticultural varieties. These cultivars, many of them originally selections from native stands of *C. illinoënsis* but later from selective crossing, have formed the basis of the pecan industry of the southeastern and south-

central United States. Grown best on deep, loose, well-drained, well-aërated soil, *C. illinoënsis* can properly be considered a multipurpose species. The trees provide food for man as well as wildlife, they are suitable for landscaping, and the wood is widely used in the manufacture of tools, lumber, and veneers. The seeds are high in caloric value and have large amounts of unsaturated oils (ca. 72 per cent), protein (ca. 11 per cent), and carbohydrates (ca. 13 per cent).

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2. **Juglans** Linnaeus, Sp. Pl. 2: 997. 1753; Gen. Pl. ed. 5. 431. 1754.

Aromatic, resinous trees of temperate or subtropical habitats; bark furrowed, scaly; wood durable, dark-colored; branchlets terete, stout, with

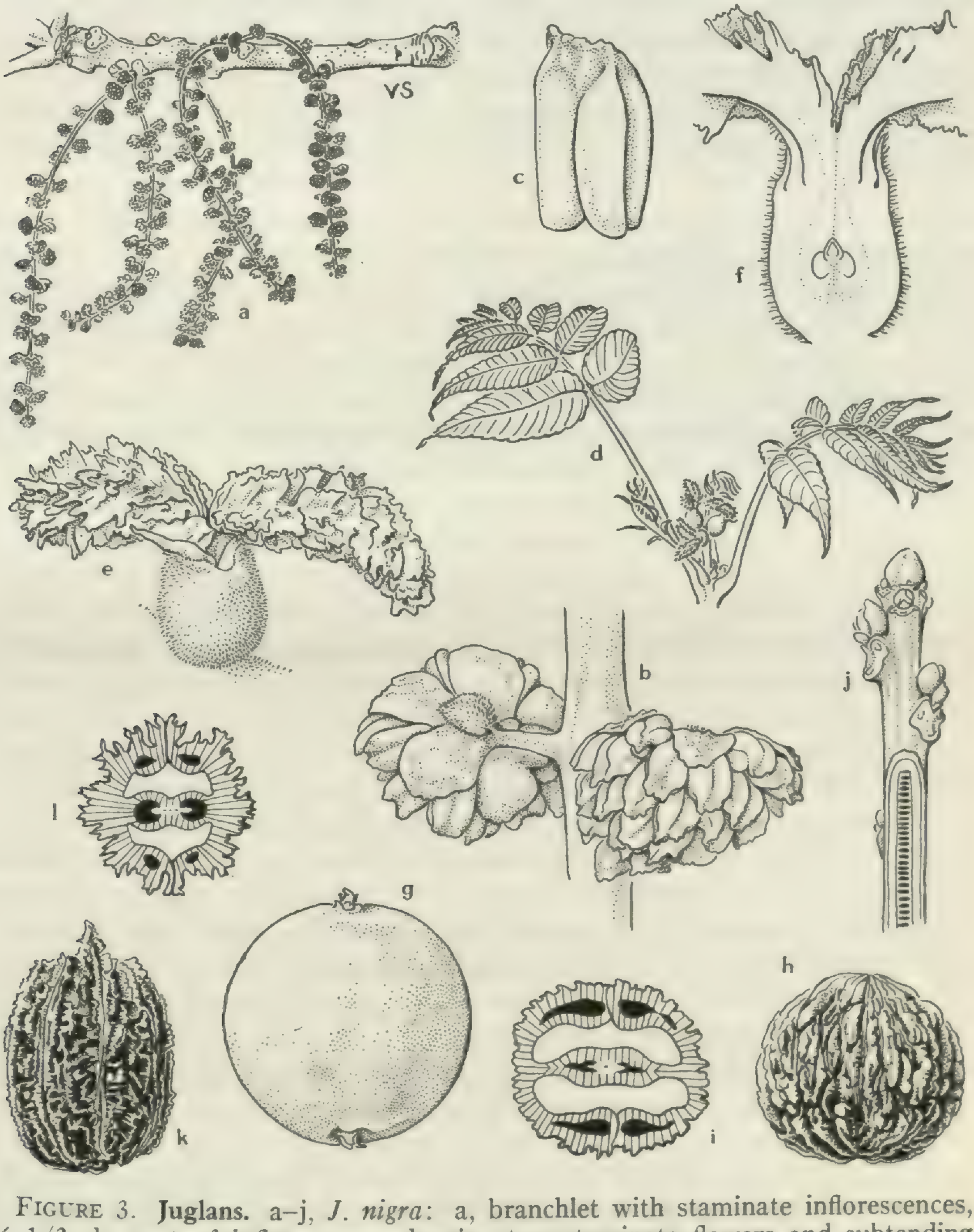

FIGURE 3. **Juglans.** a–j, *J. nigra*: a, branchlet with staminate inflorescences, × 1/2; b, part of inflorescence showing two staminate flowers and subtending bracts oriented as in "a", × 6; c, stamen, × 15; d, branchlet with terminal carpellate inflorescence, × 1/2; e, carpellate flower, × 3; f, semidiagrammatic longitudinal section of carpellate flower showing ovule, perianth, and involucre, × 4; g. mature fruit with indehiscent involucre, × 3/4; h, mature nut, × 3/4; i, median cross section of nut, cotyledons unshaded, lacunae in wall and septum black, × 3/4; j, terminal branchlet in winter condition with lower part in longitudinal section to show chambered pith, × 1. k, l, *J. cinerea*: k, mature nut without involucre, × 3/4; l, median cross section of nut, cotyledons unshaded, lacunae black, × 3/4.

chambered pith; terminal buds short to long, usually with 2 pairs of opposite scales, the inner scales accrescent, the axillary buds ± flattened, with 4 ovate scales. Leaves rarely paripinnate, few- to many-foliolate; petioles terete, canaliculate above, often swollen basally, the leaf scars large, conspicuous, elevated, obcordate, 3-lobed; leaflets conduplicate in vernation, usually ovate, acute to acuminate at the apex, generally oblique at the base, membranaceous, serrate or entire, sessile to short-petiolulate, pinnately veined. Flowers vernal, usually opening after the leaves unfold. Staminate flowers sessile or pedicellate, in many-flowered aments borne singly or in pairs from the lower axillary buds of the upper nodes, appearing from between the persistent bud scales; perianth 3–6-lobed, adnate to the ovate bract (FIGURE 3, b); stamens 8–40, inserted on the perianth in 2 to many rows, the alternately ranked stamens alternate with the lobes, the filaments free, short, the anthers erect, oblong, a conspicuous connective usually present; ovary lacking. Carpellate flowers borne in few-flowered terminal spikes on branches of the year, the ovary of each flower inclosed by and adnate to a floral envelope composed of a villous involucre and a perianth, the involucre made up of a primary bract (often free to near the base or fused to the secondary bracts) and two secondary bracts (usually free only at the apex), the bracts often laciniate at the apex, the four perianth lobes longer than the lobes of the involucre, appearing to come from the upper part of the ovary. Gynoecium 2(rarely 3 or 4)-carpellate, 1-locular at the middle, 4-locular at the very base, a major septum dividing the lower part of the locule and a secondary septum (perpendicular to the major septum) bisecting each of these divisions at the very base of the ovarian cavity; stigmas large, spreading, often clavate, fleshy, fimbriately papillate. Fruit globose, ovoid, or pyriform, occasionally obscurely 4-angled, the husk (formed mainly from involucral tissue) indehiscent, ± fleshy, glabrate to hirsute; nut globose to ovoid, often slightly flattened, indurated (the wall formed mainly from the ovarian wall, in our species thick and with lacunae in both wall and septum), longitudinally and irregularly rugose, 2-valved (upon germination), each valve inclosing half of each cotyledon, ± ribbed on the one or both sutures. Seed with a thin seed coat covering the large embryo, ± laterally compressed, shallowly or deeply lobed at the base, each cotyledon 2-lobed, filling the cavity of the nut; hilum minute, basal. Basic chromosome number 16. (*Wallia* Alef., *Regia* Loud.) LECTOTYPE SPECIES: *J. regia* L.; see Nuttall, Gen. N. Am. Pl. 2: 220. 1818; Britton & Brown, Illus. Fl. No. U.S. ed. 2. 1: 578. 1913. (Classical Latin name for walnut, *Juglans regia*, derived from *Jovis*, of Jove or Jupiter, plus *glans*, acorn.)

A genus of 18 to 20 species of temperate and subtropical regions of Europe, Asia, and the Americas. Six species are known from the United States; of these, the two in our area, *Juglans nigra* L. and *J. cinerea* L., are the only important forest species. *Juglans Hindsii* R. E. Sm. and *J. californica* S. Wats., $2n = 32$, are Californian (central California and coastal southern California respectively), while *J. major* (Torr. ex Sitzgr.)

Heller occurs from central and southwestern Texas to southwestern New Mexico and central Arizona and (as var. *glabrata* Manning) south to Guerrero, Mexico, and *J. microcarpa* Berl., $2n = 32$, ranges from western Oklahoma and western and southern Texas to northeastern Mexico. Manning (1957, 1962) also recognizes *J. pyriformis* Liebm., *J. hirsuta* Manning, and *J. mollis* Engelm. in Mexico. *Juglans Steyermarkii* Manning is endemic to Guatemala, and *J. olanchana* Standl. & Williams extends from Nicaragua to Guatemala with a disjunction (var. *Standleyi* Manning) in Colima and Jalisco, Mexico. The misnamed *J. jamaicensis* C. DC., $2n = 32$, occurs in Cuba, Hispaniola, and Puerto Rico. *Juglans* recurs in the Andes with some five species distributed from Colombia and Venezuela south to Peru, Bolivia, and Argentina. *Juglans regia* L. is native from southeastern Europe to India (and perhaps Central Asia) but is widely planted in many other temperate climates of the world. *Juglans cathayensis* Dode, *J. cordiformis* Maxim. (including *J. ailantifolia* Carr., *J. Sieboldiana* Maxim. non Göppert), $2n = 32$, *J. mandschurica* Maxim., $2n = 32$, and *J. stenocarpa* Maxim. represent the genus in eastern Asia.

In the subgeneric classification proposed by Dode (1909), who recognized many more species, *Juglans regia* constitutes sect. JUGLANS (§ *Dioscaryon* Dode), and *J. cinerea* is alone in sect. TRACHYCARYON Dode. All of the other Old World species are placed in sect. CARDIOCARYON Dode and the other New World ones in sect. RHYSOCARYON Dode.

The black walnut, *Juglans nigra* L. (*Wallia nigra* (L.) Alef.), $2n = 32$, occurs from western Massachusetts, central Vermont, and southern Ontario to southern Minnesota and southeastern South Dakota, south through eastern Nebraska to western Oklahoma and eastern Texas, and to northwestern Florida and Georgia (see Little, 1971, *map 134-E*). A plant of low altitudes, *J. nigra* grows best on deep well-drained soils, including good bottomlands. It can be found in mixed mesic forest, but rarely in pure stands. This species is easily distinguished by the lower surface of the leaflets and petioles being minutely downy with solitary or paired hairs, by the notched leaf scars that lack a fringe of hairs, and by the spherical fruit. Varietas *oblonga* (Marsh.) Fern. differs only in having ellipsoidal fruits. Flowering in early spring as the leaves appear or slightly afterward, the trees are apparently self-fertile, but individual trees have varying degrees of proterandry or proterogyny. Cross pollination usually insures better seed set and higher fruit yields.

Distributed over much of the northeastern United States, *Juglans cinerea* L. (*Wallia cinerea* (L.) Alef.), butternut, $2n = 32$, occurs from western New Brunswick, New England, southern Quebec, and southern Ontario to Wisconsin and Minnesota, south to northern New Jersey, Virginia, North Carolina, northwestern South Carolina, northern Georgia, Alabama, and Mississippi, Arkansas, and Missouri (see Little, 1971, *map 133-E*). Apparently growing best on streambanks and on well-drained gravelly or rocky soils, this species, like *J. nigra*, occurs sparingly throughout its range. It is found in many mesic forests, but it is better adapted to limestone soils than *J. nigra* is. *Juglans cinerea* is characterized by its

leaflets, downy with fascicled hairs, especially beneath; by the branchlets and petiole downy with glandular hairs; by the leaf scars with a hairy fringe along the upper margin; and by the ellipsoidal fruit.

Juglans appears to be a homoploid genus with $2n = 32$ (eleven species). *Juglans nigra* and *J. cinerea* are not known to hybridize, but hybrids of *J. nigra* with *J. Hindsii* and *J. regia* and of *J. cinerea* with *J. cordiformis* and *J. regia* have occurred under cultivation or have been produced artificially. Hybrids of *J. regia* with *J. Hindsii* and *J. cordiformis* are also known.

The characteristic chambering of the pith in *Juglans* was shown by Harlow (1930) in *J. nigra* and *J. cinerea* to be formed at the end of the growing season. In spring the young twigs of the year still have homogeneous pith. Chambering in *J. nigra* begins in late August, but in *J. cinerea* not until late September or early October. The first sign of chambering is a change in the color of the pith, followed by the formation of several cavities near the base of the year's growth (after elongation has ceased) and then throughout the twig.

Both prodigious pollen producers, *J. nigra* and *J. cinerea* were suspected of contributing to spring pollen allergies, but since neither occurs abundantly anywhere, it is doubtful that either is of importance in this connection. The pollen grains are 2-celled when shed. The pollen is relatively variable but is basically tectate, periporate, and heteropolar with the (2–)6–18(–37) pores restricted to one polar hemisphere and occasionally overlapping (Whitehead, 1965). An increase in pollen size and in pore number, as seen in *J. regia* and *J. nigra* may be indicative of specialization within the genus.

Unlike genera of the Fagaceae and Betulaceae, in *Juglans* the ovule is well developed at the time of pollination, with fertilization occurring 4–8 days later. Nuclear endosperm has been reported in *J. regia* (Nast, 1935, 1941) with approximately 1000 free nuclei present before cell wall formation occurs. Embryogeny in *J. mandschurica* is of the Asterad type (Langdon, 1934). Polyembryony has been reported in *J. nigra*.

After flowering the fruits of our species mature in September or October of the same season, dropping shortly after the leaves fall. Hypogeous germination usually occurs the following spring with a strong taproot produced by the seedling.

Although Berry (1923) suggested that *Juglans* leaves have been found in Middle Cretaceous deposits, verifiable remains occur only from the Upper Cretaceous to the present. Apparently *Juglans* was much more widely distributed over the Northern Hemisphere in the past, especially during the Eocene, Miocene, and Pliocene.

It has long been known that certain plant species have reduced growth rates and/or reduced reproductive success when growing under or close to plants of certain species of *Juglans*, e.g., *J. nigra* and *J. regia*, but not *J. cinerea*. The inhibitory substance produced by these species has been determined to be juglone, $C_{10}H_6O_2$, a red crystalline compound, that is produced by oxidation of hydrojuglone, a water soluble substance pro-

duced in the leaves, fruit, husk, bark, and perhaps the roots. This substance apparently can be washed from the leaves into the ground by rain. This general phenomenon, allelopathy, the inhibition of one plant by a substance or substances secreted by another has only relatively recently received serious attention from ecologists (cf. Muller, 1969). Other examples have been discovered in several unrelated families, including the Gramineae, Simaroubaceae, Myrtaceae, Labiatae, and Compositae.

The beautifully grained brownish wood of *Juglans nigra* is perhaps the foremost cabinet wood of North America; that of *J. cinerea* is considered to be less valuable. Selected strains and cultivars of *J. nigra* (more than 100) have been developed, mostly for nuts with larger, thinner shells that will crack easily and for low seed-abortion rates. The seeds are used largely in ice cream and confectionery and as a flavoring. The nuts of *J. cinerea* are occasionally used locally but are not commercially important. A few cultivars, based on foliage characters, have been selected as ornamentals. The European *J. regia* is the principal source of walnut lumber and nuts in the Old World. It is successfully grown in various parts of the United States and is extensively cultivated in the mild climates of California.

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Under family references see Baillon (p. 405), Berry (pp. 73–80), Conde & Stone, Fowells (pp. 202–210), Hutchinson (p. 139), Jaynes (pp. 203–211, 212–223), Kurz & Godfrey (pp. 36–38), Little (1953, pp. 213–215; 1971), Sargent (1922, pp. 169–176), Whitehead (1963, 1965), and Vines (pp. 123–127).

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REVISION OF STENOPETALUM (CRUCIFERAE)

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OF THE SEVERAL GENERA OF Cruciferae endemic in Australia, the most striking is *Stenopetalum*, a genus of eight species characterized by flowers in which the calyx is erect and closed and the narrow petals are drawn out into a long, slender and often twisted tip. Flowers of this general sort are seen in some American genera such as *Schizopetalon* and *Lyrocarpa*, but it is a type not common in the Cruciferae and among Australian genera these elongated petals are so distinctive that each species of *Stenopetalum* was initially described in that genus and none has undergone the nomenclatural vicissitudes of other Australian members of this family. Similar flowers occur in *Carinavalva glauca* Ising, but this rare species, seemingly restricted to a small area in the far north of South Australia, has many-seeded obcompressed siliques, a fruit type not found in *Stenopetalum*.

Stenopetalum lineare was the first Australian species of this family known to science, the specimens brought back by Robert Brown who served from 1801 to 1803 as naturalist under Matthew Flinders on H. M. S. *Investigator*. Flinders' charge, politically motivated and intended to forestall French activity in Australian waters, was to complete the survey of the coast of New Holland and it is interesting that his orders from the Lords Commissioners for the Admiralty included detailed instructions for the construction on the quarter deck of the *Investigator* of a "plant cabin," intended for "such plants, trees, shrubs, &c., as they [the naturalist and the gardener] may think suitable for the *Royal Gardens at Kew* . . . ." After one and one-half years of exploration the *Investigator* was pronounced unfit for the return voyage to England so the living plants collected by Brown and Peter Good, the gardener, were transferred at Sydney to H. M. S. *Porpoise*. Fortunately Brown and his artist, Ferdinand Bauer, remained in New South Wales, retaining there the bulk of the dried collections, for the *Porpoise* and the living plants were lost — wrecked on the Great Barrier Reef. Brown returned to England in 1805 and the collections became the basis for his *Prodromus Florae Novae Hollandiae*.

During Brown's years in Australia he became familiar with some of the most spectacular plants of the flora and it is perhaps understandable that he was not impressed by Australian Cruciferae. His published work makes only the briefest reference to the family, and although Brown recognized *S. lineare* as representing a distinct genus, he did nothing with the material and finally passed it on to De Candolle for description in *Systema Naturale*. The next species described, *S. robustum* of Western Australia, was correctly placed by Endlicher in *Stenopetalum* as were the species subsequently described by Mueller and by Bentham. However,

of three species figured during the 1840's in *Icones Plantarum* and described by one or the other of the Hookers in *Stenopetalum*, two are now referred to *Menkea* Lehm. and one is the widespread halophyte *Hutchinsia procumbens*.

MORPHOLOGY AND BIOLOGY

Most species of *Stenopetalum* are annuals, although *S. decipiens* of central Australia is a woody perennial and a coastal form of the widespread and variable *S. lineare* is woody and perennial. The genus is represented in all states, including Tasmania, and in the Northern Territory and is predominantly Eremaean although *S. robustum* of Western Australia is coastal in habitat and there is the coastal form of *S. lineare* just mentioned. With the exception of *S. robustum*, in which the valves are compressed parallel to the septum, all species have short siliques which are globose to (ob-)ovoid and round in section. The pedicels are variable in length and orientation and provide some useful diagnostic characters. The seeds of all species are strongly mucose when moistened, the thick perisperm immediately producing a broad band of radiate mucus. Except in the tuberculate or verrucose seeds of *S. nutans* and *S. velutinum*, the testa is smooth and there are otherwise no characters of real diagnostic or taxonomic value observable in the seeds.

Pubescence is quite variable. *Stenopetalum decipiens*, *S. velutinum*, and *S. lineare* are pubescent with irregularly branched trichomes. Those of the first two species are nearly sessile with very long, horizontally spreading rays which in *S. decipiens* are almost inextricably interwoven into a dense felt. Trichomes of *S. lineare* are similar but smaller and less elaborately branched. *Stenopetalum nutans* is unique in the genus in being sparsely pubescent with malpighiaceous trichomes. The other four species are apparently glabrous, papillose, or pubescent with simple trichomes. This represents a difference of degree rather than of kind and on plants of *S. robustum* and *S. filifolium* there can be both papillae and short, simple, rather crinkled trichomes. The cauline leaves are generally entire or dentate in *S. velutinum*, *S. decipiens*, *S. robustum*, *S. filifolium*, and *S. nutans*; *S. anfractum*, *S. lineare*, and *S. sphaerocarpum* have lower cauline leaves which are pinnatisect or trifid as in some species of *Arabidella*, although in all three the upper leaves may be entire and the coastal form of *S. lineare* includes plants with all the cauline leaves entire.

Although all species have elongated petals there is a marked variation in size, from the 3 to 4 cm. long petals of *S. nutans* and of some forms of *S. robustum* to the 5 mm. long petals of *S. sphaerocarpum*. *Stenopetalum robustum* and *S. filifolium*, both of Western Australia, have white or brightly colored yellow to orange petals, but the other six species are unusual in the family in that the petals are dully colored and range from olive-green through purplish to chocolate-brown. In all species the elongated tips are circinnately coiled in the bud. As anthesis proceeds the uncoiling of the petals forces open the sepals at the apex of the bud, al-

though they never spread widely and the calyx remains closed. In no species are the nectaries particularly well developed and the glandular tissue never completely encircles the ovary and stamens. It usually is present only around the single stamens although there is sometimes a lobe between the members of the paired stamens. This occurs occasionally in most species. Plants from the northern part of the range of *S. robustum* do show a peculiar development of the glands so that on either side of each single stamen is a flat protruding lobe of tissue. This is conspicuous both in flower and fruit and can be useful in distinguishing *S. robustum* from *S. filifolium* when the plants are only in flower. In *S. filifolium* there is development of glandular tissue above the point of insertion of the single stamens; this is shelf-like and although sometimes bilobed is never the "horseshoe" seen in *S. robustum*.

Examination with the scanning electron microscope of pollen of four species has shown it to be subglobose to ovoid, tricolpate and coarsely reticulate, the lumina large and the muri correspondingly narrow. It is hoped to examine the pollen of remaining species in the course of a more comprehensive survey of pollen types in the family.

Six species of *Stenopetalum* have been grown under greenhouse conditions, *S. nutans* at the Botanic Garden, Adelaide and *S. sphaerocarpum*, *S. velutinum*, *S. lineare*, *S. anfractum*, and *S. decipiens* at Harvard University. Of these species, all except *S. decipiens* are self-compatible, and *S. lineare* and *S. sphaerocarpum* sometimes produce cleistogamous flowers. In normal flowers, the anthers dehisce just as the uncoiling of the petals begins and at the time that the apex of the calyx has been forced open, pollen has been shed. I have seen in the field flowering plants of all species except *S. decipiens*, but I have never seen them visited by insects. The only species with scented flowers is *S. robustum*, the odor described by some as "vanilla-like," by others as "musty." Self-compatibility is advantageous to plants of an environment so inhospitable as central Australia where the capacity for seed production and dispersal from small populations or from a single plant during favorable seasons, not of regular occurrence, is of prime importance. It is true also that self-compatibility and the potential for autogamy greatly increases the chance that a species will reach suitable habitats more and more peripheral from its center of origin. In central Australia such habitats are isolated and the capacity for autogamy may be associated with the distribution of species such as *S. nutans*, *S. anfractum*, and *S. sphaerocarpum*, sparsely spread across South Australia and the Northern Territory into some very arid parts of Western Australia.

INTERSPECIFIC RELATIONSHIPS

Relationships among the species must be considered in the light both of present distribution and of post-Pleistocene climates in Australia. It is generally agreed that at some time between the late Pleistocene and the mid-Recent, Australian biota were greatly affected by the onset of

a period of severe aridity, during which the vegetation of central and south-central Australia was hard hit and, perhaps, nearly wiped out, some species retreating into southeastern Australia, others surviving in refugia in the ranges of central Australia (Crocker & Wood, 1947). This "Great Arid Period" was followed by two or three pluvial/arid (but less severely so) cycles during which there was a gradual advance of vegetation from less severely affected areas and from the refugia into present-day arid Australia.

Chromosome counts (see TABLE 1) indicate two haploid numbers, 4

TABLE 1. **Chromosome Numbers of Stenopetalum species**

SPECIES	N	2N	COLLECTION NUMBER AND LOCALITY	SELF-COMPATIBLE
S. anfractum		10?,12?	*Shaw 654* Western Australia	yes
S. decipiens		8	*Nelson 1814* Northern Territory	no
S. filifolium		5 II + I *	*Turner 5367* * Western Australia (as *S. croceum* Bunge)	
S. lineare	5 *	10	*Turner 5297* * Western Australia	
			Beauglehole 20701 Northern Territory	yes
S. sphaerocarpum	5	10	*Shaw 664* Western Australia	yes
S. velutinum	4	8	*Eichler 17563* South Australia	yes

* Turner (1967).

and 5, in the genus. The number in *S. anfractum* probably is 5, although repeated attempts to obtain a clear figure in root tip cells were unsuccessful and the somatic count is given as questionably 10 or 12. The counts of $2n = 8$ for *S. decipiens* and *S. velutinum* do corroborate the morphological evidence which sets apart these species from the others. These two densely pubescent species, *S. velutinum* and *S. decipiens*, have a center of distribution in the central Australian ranges and the present distribution is not inconsistent with advance from a refugium in the MacDonnell — Kirchauff — George Gill system, although both species show a disjunction between south-central Queensland and the area north and west of the Simpson Desert dune systems. The annual and self-compatible *S. velutinum* is far more widely spread than is the perennial and apparently self-incompatible *S. decipiens* and is found as far south as Ooldea in South Australia and westward at least to the vicinity of Laverton in Western Australia. Another cluster of related species is formed by the

Eremaean species, *S. lineare*, *S. anfractum*, and *S. filifolium* (all probably with a base number of 5). The last species differs in having brightly colored petals and I include it here with some hesitation for the floral structure is much like that of some forms of *S. robustum*. However, these three species do have in common more or less oblong siliques on short, erect or spreading pedicels. *Stenopetalum lineare* which now is widely spread and common in central Australia is represented also in South Australia, Tasmania, and Victoria by a coastal form which may have been geographically distinct since the Recent aridity. *Stenopetalum robustum* of the Southwestern Province of Western Australia is the only species to have compressed siliques, while *S. sphaerocarpum*, although represented by populations scattered across southern Australia, is neither coastal nor truly Eremaean and differs morphologically with very small flowers and globose siliques on rigidly spreading horizontal pedicels. *Stenopetalum nutans*, a large-flowered Eremaean species with pendent obovoid siliques and malpighiaceous trichomes, also stands somewhat isolated morphologically. The discontinuities in morphology among these species and groups of species support the view that they are the remnants of a more highly developed pattern of speciation, disrupted during the arid period or periods, which cannot now be satisfactorily reconstructed.

INTERGENERIC RELATIONSHIPS

Although *Stenopetalum* is a distinctive genus, its generic relationships are even less clear than are those among the species. In Schulz's (1936) treatment of the family the genus appears as the monogeneric tribe Stenopetaleae. Schulz's diagrammatic *Stammbaum* shows the Stenopetaleae diverging from the main stock of the family just below the point at which the Hesperideae and Sisymbrieae are split off. If, in using Schulz's key to the tribes, one ignores as a diagnostic character the elongated petals of *Stenopetalum*, the genus falls between the predominantly Asian Hesperideae, characterized by flowers with erect sepals and elongated siliques with bilobed stigmas, and the very large tribe Sisymbrieae which in Schulz's treatment is a catch-all for those genera with notorrhizal embryos and more or less elongated siliques which do not clearly belong elsewhere.

The genus is basically Eremaean and thus belongs to an Australian floristic element of uncertain origin. Burbidge (1960) suggested that endemic genera among the Eremaean Cruciferae, Chenopodiaceae, Compositae, and Aizoaceae are derived from a littoral or sand dune flora present during the Cretaceous when Australia was dissected by epeiric seas, elements of which flora might have reached Australia from the northern hemisphere by migration along the shores of the Tethys Sea. In addition to weaknesses in this theory pointed out by Burbidge herself, the most recent reconstruction of Pangaea (Dietz & Holden, 1970) indicates that even by the end of the Jurassic, land breakup in the Southern Hemisphere was so far advanced that the Australian landmass was attached only to

Antarctica. Prantl (1891) had placed *Stenopetalum*, along with *Menkea*, in a subtribe of the Schizopetaleae, associated with American genera such as *Mancoa*, *Tropidocarpum*, *Matthewsia*, and *Schizopetalon*. The other subtribe, Physariinae, recognized by Prantl is entirely American including *Lesquerella*, *Physaria*, and *Synthlipsis*. Although much of Prantl's system is fantasy, part of it described by a later author as "ein phylogenetisches Unding," it may be that he was in this case nearer the truth than was Schulz. However, many of the more than 370 genera in this family are the termini of otherwise extinct evolutionary lines, a situation which makes so difficult the delimitation of tribes in the Cruciferae. In the absence of evidence to the contrary, it is best to regard *Stenopetalum*, geographically isolated in Australia, as one such endpoint, the nearest related genus being, perhaps, *Menkea*.

COMMON NAMES AND USES

Stenopetalum is of no economic significance save that in favorable seasons in central Australia some species such as *S. lineare* occur in such abundance that they become part of the diet of the aboriginal population. The central Australian species are highly flavored and quite hot and probably are used both for their nutritive value and mustardy taste. Cleland & Tindale (1954) report that seeds of *S. lineare* were eaten at Yalata on the Great Australian Bight, while Cleland & Johnston (1937) noted that in the Musgrave Ranges of South Australia *S. velutinum*, called "unmuta" by the Pitjanjara, is cooked on hot stones with grass, the leaves then stripped off and eaten. However, natives at Haast's Bluff in the Northern Territory informed Cleland & Tindale (1959) that both *S. lineare* and *S. nutans* are fit only for emus and are too strong for human consumption; *S. lineare* "makes you giddy if you try to eat it." However, it may be *S. anfractum* here referred to; both species occur at Haast's Bluff and are mixed, under the name *S. lineare*, in Cleland's collections. The name for *S. lineare*, *S. nutans*, and *S. velutinum* used by members of the Pitjanjara, Pintubi, and Aranda tribes is "unmuta," "'enmerta" or something similar, although Johnston & Cleland (1942) recorded "karra garra" and "kara-kara" for *S. lineare* at Ooldea in South Australia.

ACKNOWLEDGEMENTS

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SYSTEMATIC TREATMENT

Stenopetalum R. Br. ex DC. Syst. Nat. 2: 513. 1821.

Plants erect glabrous or pubescent annuals or perennials; basal leaves, if present, pinnately divided, but often lost early in the life of the plant; cauline leaves pinnatisect or trisect or entire; inflorescences ebracteate, the buds usually ellipsoid, sometimes globose; aestivation circinnate; sepals erect (the calyx closed), the lateral saccate; petals white to orange or brown to olive-green, unguiculate, the blade elongated and often produced into a long narrow tip; stamens erect, tetradynamous; glandular tissue variable; ovules 4–20 per locule; siliques completely dehiscent and bilocular, globose, ellipsoid or (ob-)ovoid, round or compressed parallel to the septum, glabrous on the interior and exterior; septum entire; styles very short or obsolete; stigmas depressed-capitate; seeds oblong to ellipsoid and flattened, copiously mucose when moistened; embryo notorrhizal or pleurorrhizal.

TYPE SPECIES: *Stenopetalum lineare* R. Br. ex DC., Syst. Nat. 2: 513. 1821.

KEY TO THE SPECIES

A. Plants glabrous, papillose or, if pubescent, the trichomes simple or malpighiaceous.
  B. Pedicels erect or divaricately spreading at maturity.
    C. Main stems clearly anfractuose; cauline leaves pinnatisect with linear segments; petals purplish or olive-green; pedicels 4–10(15) mm. long. ..... 2. *S. anfractum.*
    C. Main stems nearly straight; all cauline leaves entire and filiform or remotely dentate; petals bright yellow-orange; pedicels 3–4 mm. long. ..... 3. *S. filifolium.*
  B. Pedicels recurved or horizontally spreading at maturity.
    D. Siliques globose or obovoid, round; petals greenish or brownish.
      E. Pedicels 3–8 mm. long and stout, usually horizontally spreading; plants glabrous or papillose; siliques globose. ..... 4. *S. sphaerocarpum.*
      E. Pedicels 8–15(20) mm. long and slender, recurved; plants pubescent with malpighiaceous trichomes; siliques obovoid. ..... 5. *S. nutans.*
    D. Siliques orbicular to ellipsoid or obovoid, compressed parallel to the septum; petals white, yellow or orange. ..... 6. *S. robustum.*
A. Plants pubescent with irregularly branched or stellate trichomes.
  F. All parts, including leaves, densely pubescent; all leaves entire or remotely dentate; sepals with gibbous thickening at the tip.
    G. Plants annual; ovules 10–20 per locule; siliques 4–7 mm. long, seeds tuberculate. ..... 8. *S. velutinum.*
    G. Plants perennial, woody at the base; ovules 3–10 per locule; siliques 7–11 mm. long; seeds smooth. ..... 7. *S. decipiens.*
  F. Upper parts of plant glabrous or sparsely pubescent; lower cauline leaves pinnatisect to trisect; sepals not thickened at the tip. ..... 1. *S. lineare.*

1. **Stenopetalum lineare** R. Br. ex DC. Syst. Nat. **2**: 513. 1821.
MAP 1.

HOLOTYPE. Victoria? Hab. in orâ australi Novae-Hollandiae, *R. Brown* (G–DC); isotypes? (BM, E, MEL, P).

S. lineare var. *canescens* Bentham, Flora Austral. **1**: 78. 1863. Holotype. Victoria. Port Phillip, *F. Mueller* (K).

Plants annuals or, in coastal sites, often perennial, subglabrous to densely pubescent; trichomes sessile or shortly stipitate, stellate or irregularly branched, densest toward the base of the stems; stems to at least 5 dm. high, but the height most variable, usually branched, erect or, especially in coastal plants, sometimes decumbent with erect laterals; basal leaves usually less than 5 cm. long, exceptionally to 10 cm., pinnatipartite with linear to narrowly obovate segments, these sometimes finely dentate or, in coastal plants, often entire; cauline leaves to 6 or 7 cm. long, exceptionally to 10 cm., generally pinnatisect or trisect, the uppermost sometimes entire and filiform; inflorescences rather loose, elongating before anthesis, the buds obovoid or ellipsoid; sepals 3–6 mm. long, elliptic-oblong to narrowly obovate, the lateral strongly saccate at the base; petals (4)6–13 mm. long, chocolate-brown to olive-green, the linear claw expanded into an oblong blade roughly U-shaped around the single stamens (open on the outer side); infructescences loose and elongated (to 30 cm.); pedicels less than 5 mm. long, usually nearly erect, rarely horizontally spreading or even reflexed; siliques 3.5–7.5 mm. long, oblong and terete; stigmas capitate and slightly elongated; ovules 8–14(18) per locule; seeds 0.8–1.5 mm. long, oval to oblong and compressed, the testa red- or orange-brown, smooth. $n = 5$, $2n = 10$.

DISTRIBUTION. Widely spread in the interior of southern Australia, but also found in Tasmania and on the coasts of South Australia and Victoria.

Queensland. Gilruth Plains, Cunnamulla, *Allen 626, 666* (CANB); Nockatunga Station, *Blake 11820* (BRI); Birdsville, *Blake 12211* (BRI). **New South Wales.** Milparinka, *Collier* in 1910 (NSW). Wilcannia, *Kennedy* in 1885 (MEL); West Wyalong, *Ingram* in 1958 (NE); Broken Hill, *Morris 2332* (BRI, K); Balranald, *Lucas* in 1878 (MEL). **Victoria.** Kulkyne National Park, *Beauglehole 1137* (MEL); East Whipstick near Bendigo, *Robbins* in 1948 (MEL); Werribee, *Fullager* (MEL); Murrayville, *Williamson* in 1928 (E); Mt. Arapiles, *Hicks* in 1960 (AD). **Tasmania.** Bellerive, *Lucas* in 1923 (NSW); Ralph's Bay, *Comber 1611* (E, K); R. Jordan, *Rodway* in 1898 (NSW). **South Australia.** 17 miles north of Mt. Gason bore, *Lothian 355* (AD); Frome River, 2 km. north of Marree, *Shaw 191* (AD); Koonamore, *Osborn* in 1928 (SYD); 26 km. south The Gums H. S., *Shaw 175* (AD); Port Noarlunga, *Griffith* in 1912 (AD); Beachport, *Tate* in 1882 (AD); Ross River near Ludgate's Well, *Shaw 492* (AD); 11 km. north of Mable Creek, *Shaw 522* (AD); Wudinna, *Ising* in 1938 (AD); Bitter Well, Coomaba, *Cleland* in 1929 (AD); between Tomkinson and Mann Ranges, *Cleland* in 1954 (AD); Fowler's Bay, *Richards* (AD, MEL). **Northern Territory.** 35.9 miles

s. w. Tobermory H. S., *Chippendale* (NT); Atnarpa Station, *Beauglehole 20701* (MEL); 3 km. north of Charlotte Waters, *Shaw 483* (A, AD); Haast's Bluff Reserve, *Cleland* in 1957 (AD); 40 km. west of Erldunda, *Cleland* in 1935 (AD). **Western Australia.** 5 miles south of Giles, *Kuchel 191* (AD); 3 km. north of Old Eucla, *Wilson 1647* (AD); Kalgoorlie, 5 miles along Coolgardie Road, *Burbidge 1875* (BRI, CANB); Israelite Bay, *Brooke* in 1885 (MEL); Stirling Range, *Morrison* in 1902 (K).

The type locality probably is Port Phillip Bay, visited by Brown in April, 1802, and that is the locality given on those specimens cited as possible isotypes. However, there is in the herbarium of the British Museum (Natural History) a specimen, labelled "Bass Strait" which may have been collected in the Kent Group by Brown during his stay following Flinders' departure.

Stenopetalum lineare is both the most common and the most widely spread species in the genus and is the only one known from Tasmania. Although in inland parts of Australia this species is always an herbaceous annual, plants from coastal parts of South Australia, Victoria, and Tasmania often are woody, the main stems decumbent with erect laterals, and perennial. Bentham's var. *canescens*, described as "A low branching more robust form, the young shoots slightly hoary with a minute stellate pubescence, and the leaves rather thicker," is based upon a typical plant of the coastal form, woody at the base and with the leaves mostly entire and probably quite fleshy. Although De Candolle described *Stenopetalum* (*S. lineare*) as glabrous, I have never seen plants which are completely without trichomes. The density of pubescence is, however, quite variable and older plants may have trichomes only in the leaf axils. The original (and incorrect) description of *S. lineare* as glabrous led Bentham to describe, in fact, to re-describe, the littoral form as var. *canescens*, a name which has been wrongly applied to plants from the interior, the result being confusion of *S. velutinum* with *S. lineare*.

From Tasmania and the mainland coast toward the interior can be seen a gradual change in fruit shape. Plants of the coastal form have narrow cylindrical fruit; the average ratio of silique length to width (across the replum) in the Tasmanian plants I have seen is 4.7:1. In the interior, *S. lineare* has fruit more nearly ellipsoid. The average ratio of length to width is 3.0:1 in plants of the Flinders Range and Olary Spur in South Australia and 2.4:1 in plants from the Lake Eyre basin. These plants have seeds which are larger and exude mucus more rapidly than do those of coastal plants.

To a plant of *S. lineare* goes the distinction of having been the first plant collected in Australia by Ferdinand Mueller. Mueller landed at Port Adelaide early in December, 1847 and the plant (*MEL 10781*) is labelled in his hand, "In poeinsulae Levevre oris [Port Adelaide]/Dec. 1847/F. Mueller/prima fecit planta a me in terra Australasia collecta; ex hac causa nomen triviale 'gratulatorium' adposis." Although Mueller often used the name "Stenopetalum gratulatorium" (or gratulorum) on labels, it was never published.

MAP 1. *Stenopetalum lineare* (dots); *S. robustum* var. *robustum* (triangles), var. *pedicellare* (squares).

2. **Stenopetalum anfractum** E. Shaw, sp. nov. FIGURE 1; MAP 4.

Plantae annuae, glabrae vel sparse papillosae; caules rigiduli et multum ramosi, caulo principali anfractuoso-flexuoso; folia caulinea pinnatisecta; petala olivacea vel obscure purpurea, lamina longe et anguste producta; pedicelli fructiferi brevissimi crassique; siliquae oblongae vel ellipsoideae, teretes; ovulae 8–15 in loculo. $2n = 10?$ vel $12?$

HOLOTYPE. South Australia. Ca. 25 km. west of Welbourne Hill, *Whibley 927* (AD), isotype (GH).

Plants slender annuals, glabrous or sparsely papillose; stems 1–4 dm. long, rigid, usually much branched and thus anfractuose, terete to sharply angled; basal leaves rosulate and apparently similar to the cauline leaves, but rarely present on flowering or fruiting plants; cauline leaves 1–6 cm. long, pinnatisect with 1 to 3 narrow and nearly linear lobes per side, the upper leaves sometimes entire and filiform; inflorescences rather loose and few-flowered, the buds ellipsoid; sepals 3.5–5.5 mm. long, oblong to narrowly obovate, not saccate; petals 8–13 mm. long, olive-green to

FIGURE 1. *Stenopetalum anfractum*. Habit, × 1/2.

purplish, the claw narrow but expanded into the suborbicular to elliptic blade, this elongated into a narrow tip more than half the total length of the petal; stamens 2.5–4 mm. long; glandular tissue ± square around the single stamens and subtending the adjacent paired stamens; infructescences loose, the pedicels 4–10(15) mm. long, short and stout, appressed or

slightly spreading; siliques 4–6(7) mm. long, oblong to ellipsoid and nearly terete; stigmas capitate and sometimes bilobed; ovules 8–15 per locule.

DISTRIBUTION. On sandy soils in the southern part of the Northern Territory, in South Australia to the west of Lake Eyre, and in western Australia to the longitude of Cue.

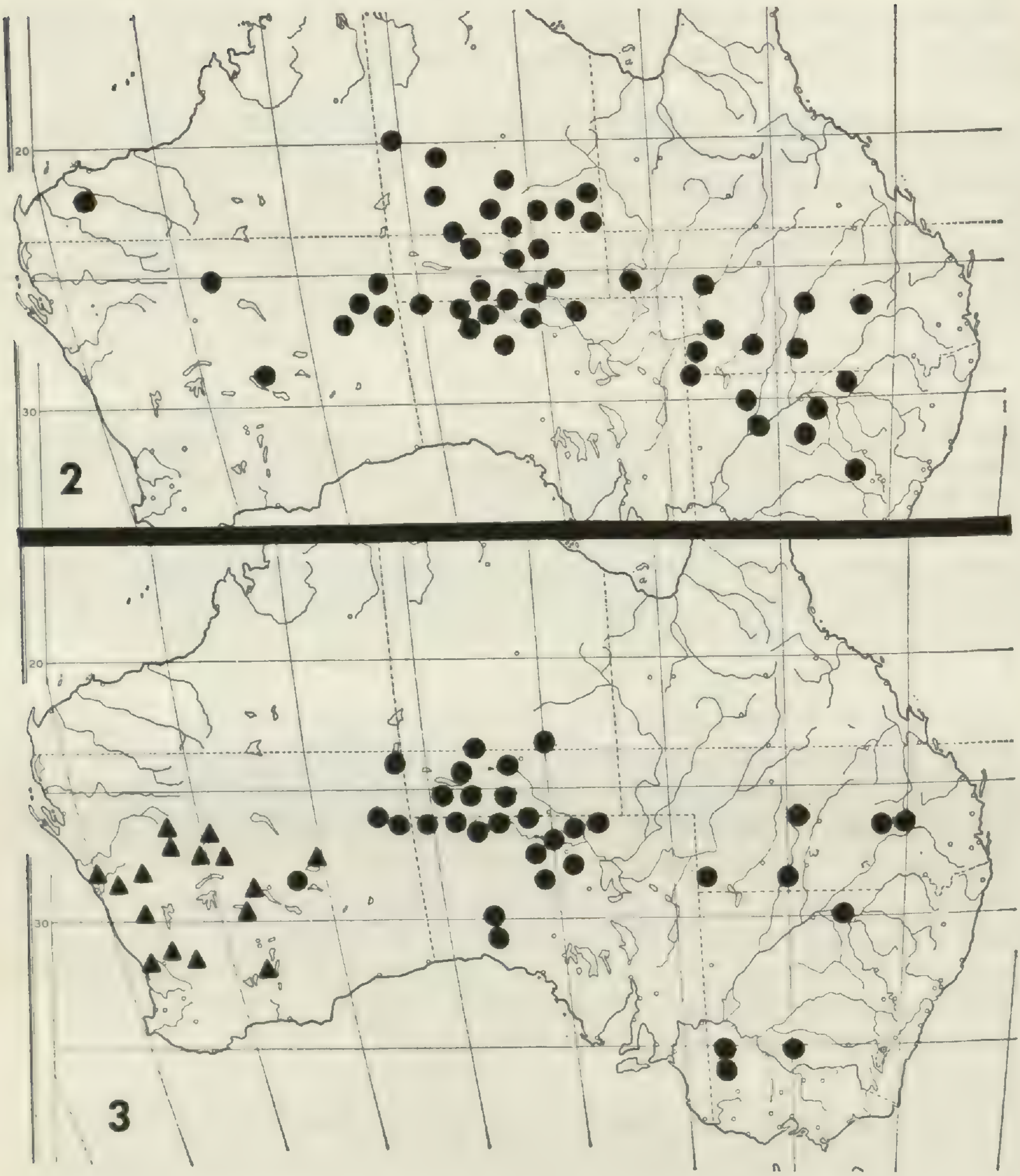
South Australia. 34 km. north of Old Lambina H. S. ruins, *Shaw 447* (A, AD); 22 km. south of Mt. Willoughby, *Shaw 516* (AD); 26 miles north of Woorong Creek, *Beauglehole 20167* (MEL); De Rose Hill Station, *Lothian 858a/54* (AD); Wild Cat Bore, 25 km. s. w. of Everard Park H. S., *Whibley 1119* (AD); Ernabella, *Cleland* in 1933 (AD). **Northern Territory.** 32 miles n. e. of McDonald Downs Station, *Lazarides 5925* (AD, CANB, MEL, NSW, NT, PERTH); 5 miles e. of Coniston H. S., *Chippendale* (AD, NT); 35 miles s. w. of Alice Springs Township, *Perry 5477* (AD, BRI, CANB, NT); the "Pudding" area, Mt. Olga complex, *Schodde 435* (AD, CANB). **Western Australia.** Giles, *Hill 1377* (AD); Mt. Squires, Barrow Range, *Helms* in 1891 (AD, MEL, NSW); 22 miles west of Browne Range, Gunbarrel Highway, *George 5408* (PERTH); 80 miles east of Meekatharra, *Gardner 7874* (PERTH); 50 miles s. e. of Gascoyne Junction, *Turner 5382c* (TEX); 48 km. south of Mt. Magnet, *Shaw 648* (AD); Cue, *Andrews* in 1903 (PERTH); 67 km. s. w. of Payne's Find, *Shaw 663* (AD).

Stenopetalum anfractum is most easily recognized by the rigid stems which are repeatedly branched, producing a distinct zig-zag effect. At the point of branching the main stem is usually D-shaped in section, with definite ridges at the angles, a character which can be of help in distinguishing *S. anfractum* from the rather similar and, in part, sympatric species, *S. lineare*. At one time I thought that this taxon was best treated as a subspecies of the Western Australian *S. filifolium*, so that material seen before 1968 was annotated as "S. filifolium ssp. anfractum," a name never published. However, I now believe that it is better treated as a distinct species which is most closely related to *S. lineare*.

3. **Stenopetalum filifolium** Bentham, Flora Austral. 1: 78. 1863.
MAP 3.

HOLOTYPE. Western Australia. Swan River, *Drummond s.n.* (K).

Plants slender annuals, glabrous or sparsely pubescent; trichomes when present, usually at the base of the stems, simple, short and more or less crinkled; stems to 40 or 50 cm. high, erect and often very fine, sometimes quite elaborately branched; basal leaves unknown; cauline leaves 1–4(7) cm. long, 1–3(5) mm. wide, rather few and scattered, entire and often filiform, rarely remotely dentate; inflorescences loose, the flowering pedicels very short and the flowers apparently subsessile, buds ellipsoid; sepals 3.5–4.5 mm. long, elliptic to oblong, the lateral saccate; petals 10–15 mm. long, bright yellow-orange, the claw linear and expanded into an oblong blade, this drawn out into an acuminate tip; stamens 2.5–3.5 mm. long; glandular tissue forming a narrow shelf on the inner side of each single stamen; infructescences usually loose, but variable; pedicels



MAP 2. *Stenopetalum nutans*. MAP 3. *Stenopetalum velutinum* (dots); *S. filifolium* (triangles).

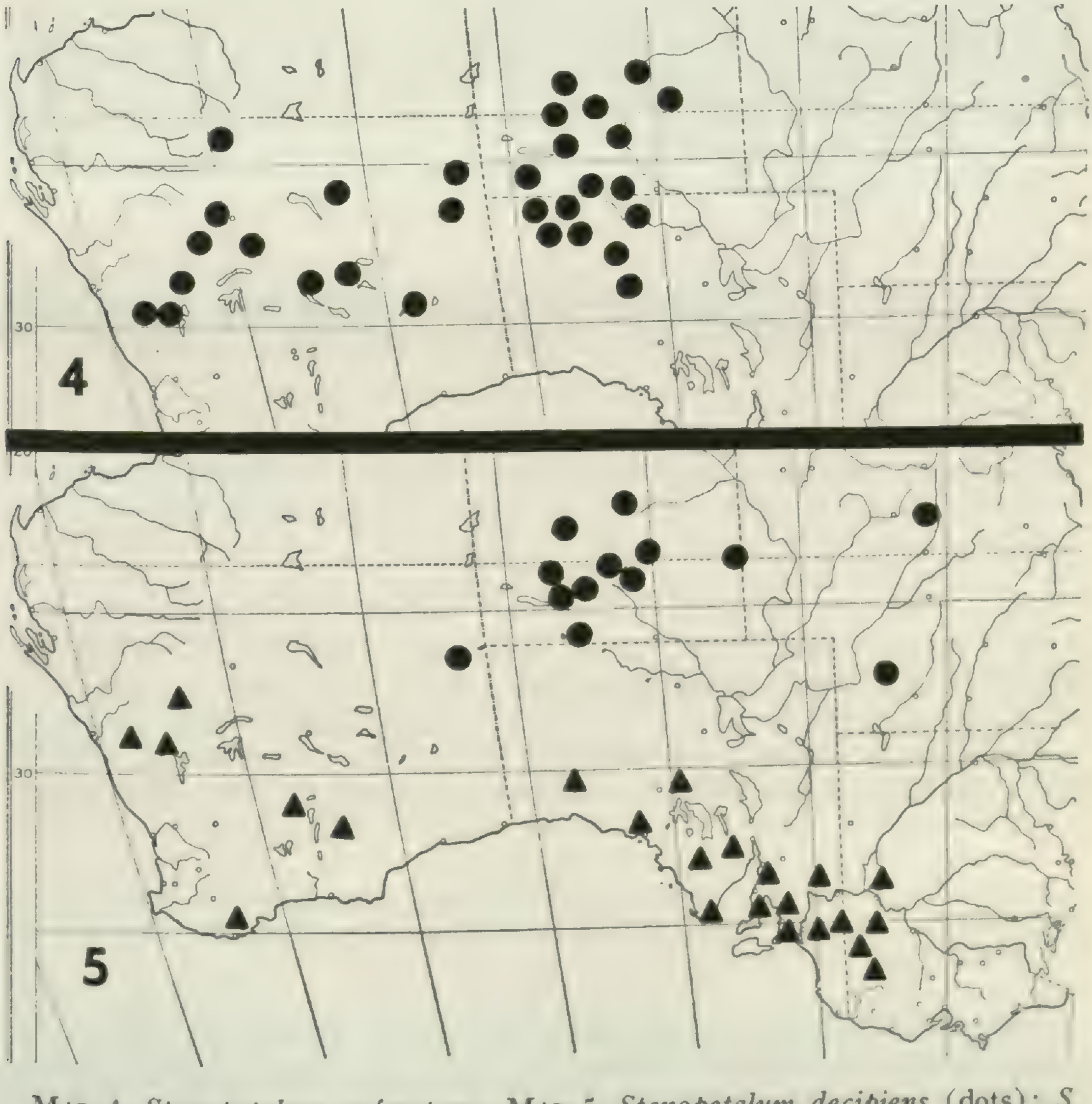
3–4 mm. long, stout and usually spreading from the axis; siliques 4.5–6 mm. long, ellipsoid and slightly compressed or terete; stigmas bilobed; ovules 6–10 per locule; well developed seeds not seen. $2n = 5\ II + I$.

DISTRIBUTION. Western Australia, in the districts of Austin, Coolgardie, Irwin, Avon, and Darling.

Western Australia. Lake Violet Station, 75 miles e. of Wiluna, *Bennett 71* (PERTH); 8 miles south of Menzies, *George 2724* (PERTH); Pioneer, *Davies 269* (PERTH); 5 miles west of Meekatharra, *Speck 579* (CANB, PERTH); 107 miles north of Mullewa, *Turner 5367* (TEX); Yalgoo, *Gardner 7756* (PERTH); 18 miles s. w. of Warriedar H. S., *Shaw 666* (AD); Merridin, *Koch 2845* (K, NSW); 77

miles north of Geraldton, *Shaw 617* (AD); Northampton, *Maiden* in 1909 (NSW); near Smith's Mill, 20 miles e. of Perth, *Andrews* in 1902 (NSW).

Stenopetalum filifolium is an attractive little plant which seems to be quite widely spread in the southern half of Western Australia. The known range overlaps, in part, those of several other species of *Stenopetalum*, but the only one with which this species might be confused in *S. anfractum*. *Stenopetalum anfractum* has leaves usually at least trisect and petals of a dull brownish or purplish color, while *S. filifolium* has narrow entire leaves and petals which are a bright, clear orange-yellow. I have collected *S. filifolium* near the Murchison River Crossing on the Northwestern Coastal Highway and at several places southwest of Mt. Magnet. In the latter area it often occurs with *S. anfractum*, but the two species could always be easily distinguished.



MAP 4. *Stenopetalum anfractum*. MAP 5. *Stenopetalum decipiens* (dots); *S. sphaerocarpum* (triangles).

4. **Stenopetalum sphaerocarpum** F. Muell. Hook. Lond. Jour. Bot. 8: 5. 1850. MAP 5.

LECTOTYPE. South Australia. Towards the entrance of the Murray River, *F. Mueller* in 1848 (MEL *10847*).

Plants slender annuals, glabrous or sparsely papillose; stems 1–3 dm. long, often straggling, and wiry and leafless when in fruit; basal leaves to 5 cm. long, pinnatifid with 2 or 3 lobes per side, narrowing gradually to the slender petiole; cauline leaves 0.5–4 cm. long, few and scattered, entire, usually trifid with the central lobe slightly longer than the laterals, tapering to a slender petiole; inflorescences few-flowered and elongate, the buds ellipsoid; sepals 2–2.5 mm. long, oblong or obovate to elliptic, the lateral ones markedly saccate; petals 3.5–6 mm. long, 0.6–1 mm. wide, olive-green or purplish, the claw suddenly expanded into the round or elliptic blade, this drawn out into a slender tip; stamens 2–2.5 mm. long; glandular tissue poorly developed, consisting of 1 or 2 small lobes on either side of each single stamen; infructescences loose, the pedicels 3–7 (11) mm. long, stout and rigid, horizontal or slightly recurved and the siliques often pendent; siliques 3–5.5 mm. long, globose or broadly obovate, slightly depressed at the base of the style; stigmas depressed and capitate; ovules (4)6–10 per locule; seeds 1.5–2 mm. long, oblong to ellipsoid and flattened, yellow- or orange-brown, the testa smooth. $n = 5$, $2n = 10$.

DISTRIBUTION. From southern New South Wales and northwestern Victoria across southern South Australia into Western Australia.

New South Wales. 120 miles south of Menindee, *G. J. White* in 1963 (NSW). **Victoria.** Lendrook Plain, Kulkyne National Park, *Beauglehole 5283* (MEL); about 10 miles east of Kiamal in the Ouyen district, *T. B. Muir 1106* (MEL); Underbool, *Malone* in 1915 (A, NSW); vicinity of Rainbow, *C. S. Sutton 1633* (MEL); near Dimboola, *F. M. Reader* in 1898 (MEL). **South Australia.** Canegrass Station, *Ising* in 1937 (AD); Kringin Reserve, ca. 32 km. north of Pinnaroo, *Wilson* in 1961 (AD); Karoonda, *Winkler* in 1934 (AD); 5 km. north of junction of Chauncey's Line and Monarto South road, *Eichler 15097* (AD); Crystal Brook, *Mueller* in 1851 (MEL); Ardrossan, *Tepper 292* (AD, MEL); Port Lincoln, *Mueller* [?] (MEL); Cunyarie Hills, *Wilson 1884* (AD); Wudinna, *Ising* in 1938 (AD); 8 miles north of Kingoonya, *Beauglehole* in 1968 (AD); Koonibba, *Cleland* in 1928 (AD); Ooldea Soak, *Cleland* in 1939 (AD). **Western Australia.** Mt. Magnet, *Fitzgerald* in 1903 (NSW); Lake Monger, southwest of Warriedar H. S., *Shaw 664* (A, AD); Morawa, *Gardner 7518* (PERTH); Swan River, *Drummond 687* (BM, E, K, MEL, P, W); basaltic ridges north of Stirlings Range, *Mueller* in 1851 (MEL); Boulder, *Staer* in 1905 (E); Camp 54, Elder Exploring Expedition [80 miles s. Victoria Springs], *Helms* in 1891 (AD, MEL).

Stenopetalum sphaerocarpum is morphologically uniform throughout the range, the small flowers and globose siliques on rigid horizontally spreading pedicels at once distinguishing this from other species of *Stenopetalum*. The flowers are the smallest of any species in this genus, for the petals although always drawn out into the characteristic elongated tip are no more than 6 mm. long. This species and *S. lineare* are the only species of *Stenopetalum* known from Victoria and southern South Australia.

5. **Stenopetalum nutans** F. Muell. Fragm. Phytogr. Austral. 3: 27. 1862. MAP 2.

HOLOTYPE. Queensland. Between Stokes Range and Coopers Creek, *F. Wheeler* (MEL *10789*).

Plants annual or, under favorable conditions, biennial, sparsely pubescent; trichomes malpighiaceous; stems usually to 3 dm., exceptionally to 5 dm. high, single to several, erect or decumbent and often much branched; basal leaves to about 6 cm. long, entire to remotely dentate or pinnatifid, narrowing to a slender petiole about as long as the blade; cauline leaves 3–9 cm. long, 4–12 mm. wide, linear to narrowly elliptic, entire or dentate toward the base; inflorescences loose and few-flowered, the buds obovoid or ellipsoid and purplish at the tip; petals 15–40 mm. long, the blade 0.8–1.5 mm. wide, yellowish green or brown, the claw 2 to 3 mm. long, expanded into an elliptic blade drawn out into a long, slender and often twisted tip; stamens 3–5.5 mm. long; glandular tissue poorly developed, consisting of a bilobed piece of tissue on the inner side of each single stamen; infructescences loose and often secund, the pedicels 7–12(17) mm. long, at maturity recurved and the siliques nutant, occasionally horizontally spreading; siliques 6–10(13) mm. long, obovoid and sometimes slightly compressed; stigmas capitate and depressed; ovules 6–12 per locule; seeds 1.5–2 mm. long, reniform, orange-brown, the testa tuberculate or verrucose.

DISTRIBUTION. *Stenopetalum nutans* is widely spread across central Australia, from Roma, Queensland, in the east to the Hamersley Range in Western Australia. It is common in the southern half of the Northern Territory and in the adjacent part of South Australia, especially to the northwest of Lake Eyre. The area encompassed by the scattered records from Western Australia suggests that *S. nutans* is widespread in the Eremaean of that state.

Queensland. Roma, *anon.* (MEL); Charleville, *Clemens* in 1945 (BRI); "Gilruth Plains," Cunnamulla, *Allen 2420* (CANB); Tenham Station, 25 miles s.s.e. Windorah, *S. T. Blake 12032* (BRI); Thargomindah, *Conacher* in 1931 (NSW); east of Camp 22 [Simpson Desert Expedition], *Crocker* in 1939 (AD). **New South Wales.** Lighting Ridge, *Constable* in 1951 (NSW); Mugincoble, 5 miles s.e. Parkes, *Constable* in 1947 (NSW); near Gongolgon, *Beadle* in 1941 (SYD); Cobar, *Beadle* in 1940 (SYD); 45 miles s.w. of Wanaaring. *Chislett 6* (NSW). **South Australia.** Abminga, *Ising* in 1933 (AD); 11 km. southeast of new Lambina H. S., *Shaw 437* (A, AD); 18 miles west of Welbourne Hill, *Beauglehole 22745* (MEL); Kenmore Park, *Cleland* in 1950 (AD); 15 km. west of Everard Park homestead, *Eichler 17422* (AD); N. Musgrave Ranges, *Basedow 257* (AD, K, NSW); Piltardi, *Wilson 2536* (AD). **Northern Territory.** 3 miles west of Argadargada H. S., *Swinbourne 570* (NT); Tarlton Downs, *Mathew* in 1955 (AD, CANB, BRI, MEL, NSW, NT); 3 km. north of Charlotte Waters, *Shaw 482* (AD); 17 miles east of Harts Range Police Depot, *Lazarides 5207* (AD, CANB, MEL, NSW, NT, PERTH); 5 miles south Taylor River Crossing, Stuart Highway, *Nelson 1250* (AD, NT); 40 miles south Aileron Township, *Perry 5366* (AD, BRI, CANB, MEL, NSW,

NT, PERTH); Rodinga, *Ising* in 1936 (AD); Tanami area, *A. W. Barks* in 1948 (NT); Mt. Doreen, *Paige & Turner* in 1964 (NT); George Gill Range at junction with Levi Range, *Beauglehole 27130* (MEL); Mulga Park H. S., *George 5131* (PERTH). **Western Australia.** Giles Settlement, *Hill 1385* (AD); 68 miles s.w. of Warburton Mission, *George 8158* (AD, GH, PERTH); Hamersley Range, *McMillan* in 1958 (PERTH); 38 miles n.e. Meekatharra, *Speck 1137* (CANB, PERTH); Glenorn Station, Malcolm, *Burbidge* in 1938 (PERTH).

Stenopetalum nutans, with large pendent siliques and long green petals, these with twisted tips, is the most distinctive species of the genus, immediately attracting one's attention in the field.

6. **Stenopetalum robustum** Endl. Enum. Pl. Hugel. 4. 1837.

Plants annuals, papillose or subglabrous, variable in size and habit; stems (of fruiting plants) 3 cm. to 1 m. long, short and robust or loose, straggling, and much branched; basal leaves to 4(8) cm. long, entire to deeply pinnatisect, usually lost early; cauline leaves to 3(6) cm. long, few and scattered, entire and linear or oblanceolate or coarsely lobed or dentate; inflorescences few-flowered and (in southern plants) often subumbellate, toward the northern part of the range, laxer; sepals 2.5–5 mm. long, elliptic-oblong to obovate, the laterals markedly saccate, all gibbous at the tip; petals 6.5–20 mm. long, variable (see discussion); stamens 2.5–5 mm. long, the anthers sometimes with a small appendage at the base of each cell; glandular tissue white to reddish, consisting of a protuberant lobe on each side of each single stamen; infructescences loose; pedicels 2–4(6) mm. long, usually recurved [7–20 mm. long in var. *pedicellare*]; siliques (4.5)5.5–9 mm. long, elliptic to suborbicular or obovoid and compressed; stigmas obscurely bilobed; ovules 6–12 per locule; seeds about 2 mm. long, oblong to suborbicular and flattened, reddish-brown.

KEY TO THE VARIETIES

Pedicels 2–4 mm., exceptionally to 6 mm. long. . . . . var. *robustum*.
Pedicels 7–20 mm. long, and very slender. . . . . var. *pedicellare*.

6a. **Stenopetalum robustum** var. **robustum**. MAP 1.

HOLOTYPE. Western Australia. King George's Sound, *Hügel* (W).

S. croceum Bunge in Lehmann, Plantae Preissianae 1: 258. 1844–45. Holotype. Western Australia. "In arenosis sylvae haud longe ab oppidulo Perth," *Preiss 1939* (P), isotypes (MEL, P, W).

S. gracile Bunge, Lehmann, Plantae Preissianae 1: 257. 1844–45. Holotype. Western Australia. "In arenosis umbrosis vallis haud longe ab ora maritima Perth," *Preiss 1938* (P), isotypes (MEL, P, W).

S. robustum var. *gracile* (Bunge) Ostenf. Kgl. Danske Vidensk. Selsk. Biol. *Medd.* 3(2): 65. 1921.

S. minus Bunge, Lehmann, Plantae Preissianae 1: 258. 1844–45. Holotype.

Western Australia. "Ad Princess Royal Harbour," *Preiss 1936* (P), isotypes (MEL).

S. album E. Pritzel, Feddes Repert. **10:** 133. 1911. Holotype. Western Australia. "In partibus australibus prope oppidulum Busselton, haud procul ab ora marina," *Max Koch 1969* (B), isotypes (MEL, NSW).

Western Australia. Murchison's River, *anon.* (MEL); Yandanooka, *A. Morrison* in 1904 (E); Nungarin, *Stoward 343* (BM); Moora, *Ashby 159* (AD, PERTH); 2 miles east of Forrestdale, *George 3039* (PERTH); 4 km. west of the Mandurah Road on the road to White Hill, *Shaw 710* (AD); Bunbury, *E. Ashby* in 1930 (AD, BM); Busselton, *Lucas* in 1928 (NSW); on limestone outcrops below the Cape Naturaliste lighthouse, *Shaw 702* (AD); 1.5 km. east of Hamelin Bay, *Shaw 688* (AD); (Lake Muir), Tourbay [Torbay, near Albany], *Mueller* (MEL).

Stenopetalum robustum is, as the synonymy suggests, the most variable species of the genus. The most conspicuous variation, that responsible for the several synonyms, is in the petals — in their color, in the absolute length, and in the relative lengths of the blade and its acuminate tip. Plants from the southernmost localities, such as the type of *S. robustum* from King George Sound, and those in the vicinity of Cape Leeuwin and Augusta have white or cream-colored petals with short and rather broad tips which are about 1 to 3 times the blade in length, or have petals which show no clear demarkation between blade and tip and are trullate. At the other extreme are the populations occurring northward from the vicinity of Mandurah (about 50 miles south of Perth). These plants have yellow to deep orange petals with very long and slender tips which may be 10 times or more the blade in length. Between the extremes occur all intermediates. A sample taken near Cape Naturaliste included plants with the short white petals of the type, plants with longer (but white) petals, plants with longer petals (only the tips orange or yellow), and some with petals entirely yellow or orange, but the tips not so long as those seen on plants growing north of Mandurah.

Plants from the southern part of the range — those with short white petals — tend to be shorter and more robust, and to have denser inflorescences, and this is generally true of those in coastal areas. Those growing inland and north of Perth, are usually large and more branched. Some plants in a collection made near Yanchep (*Shaw 529*, AD, GH) were 1 meter in height and very loose and straggling. Also noticeable in proceeding from Cape Leeuwin northward is a gradual increase in laxness of inflorescences and infructescences. Plants with compact, but slightly elongated inflorescences, look remarkably like flowering plants of *Stackhousia*.

The holotype of *S. robustum*, collected by Hügel at King George Sound (Albany, on the south coast of Western Australia) has short white petals, described by Endlicher as "Petala sepalis duplo longiora, . . . " that is, about 2 1/2 lines long. The next collections, those of Preiss, were made at Princess Royal Harbour, the western arm of King George Sound (*Preiss 1936*), and near Perth (*Preiss 1938, 1939*). From these three collections Bunge described three species of *Stenopetalum*. That from Princess Royal

Harbour is *S. minus* described as having "petalis sepala duplo superantibus (croceis) . . . " and "Caules . . . florentes 3–4 pollicares." This is rather depauperate material of the form collected by Hügel and the reference to the petals as yellow may have been a misinterpretation of dried material. Oddly enough, Bunge made no outright comparison of this "species" with *S. robustum* and he may not have realized that the localities are essentially the same. The two collections made near Perth became the types of *S. gracile* and *S. croceum*. The former is based on white-flowered plants, the petals described as " . . . sepala 3plo superantibus (albis), . . . " and as 6 lines in length. *Stenopetalum croceum* Bunge described as having petals " . . . sepala quadroplo superantibus (croceis) . . . " and 8 lines long with a long slender tip. Comments in the protologues of these three do show that Bunge understood that the plants before him were closely related to Endlicher's species and Bunge cannot be faulted for his failure to realize that the isolated collections from Perth and Albany do belong to a single species. A fifth name belonging here is *S. album* E. Pritzel, based on a collection from Busselton on Geographe Bay. The type is quite ordinary white-flowered material much like the type of *S. robustum*.

6b. **Stenopetalum robustum** var. **pedicellare** (F. Muell. ex Benth.) E. Shaw, comb. nov. MAP 1.

S. pedicellare F. Muell. ex Bentham, Flora Austral. 1: 79. 1863. Holotype. Western Australia. Murchison River, *Oldfield* (K).

Western Australia. 45 miles s.e. of Carnarvon, *Beauglehole 11754* (MEL); between Carnarvon and Shark Bay, *Berston* in 1962 (PERTH); 103 miles s.e. of Carnarvon, *Beauglehole 11783* (MEL); Lake Violet, *Speck 1301* (AD, CANB, PERTH); Twin Peaks Station, *Royce 5721* (PERTH); Champion Bay [Geraldton], *Gray 54* (MEL); Yandanooka, *Morrison* in 1904 (E); Glenorn Station, Malcolm, *Burbidge* in 1938 (PERTH).

Although described by Bentham as a distinct species, these slender plants differ from the northern form of var. *robustum* only by the more straggling habit and very long pedicels. The petals, described by Bentham as "apparently yellow" are a bright orange-yellow, much as in *S. filifolium*.

7. **Stenopetalum decipiens** E. Shaw, sp. nov. FIGURE 2, MAP 5.

Plantae perennes, suffruticosae, saepe ramosissimae, dense pubescentes trichomatibus ramosis, his in tomento coacto implexis; petala liguliformes hepatica vel olivacea; infructescentiae laxae, pedicellis divaricatis; siliquae ellipsoidea vel anguste obovatae; ovulae 5–10 in loculo; semina laeves porphyrea vel obscure aurantia. $2n = 8$.

HOLOTYPE. Northern Territory. 44 miles w.n.w. of Hartz Range Police Station, *Lazarides 5889* (AD), isotypes (BRI, CANB, MEL, NSW, NT).

FIGURE 2. *Stenopetalum decipiens*. Habit, × 1/4; detail of pubescence, × 2.

Plants perennial, usually straggling subshrubs, densely pubescent; trichomes sessile or subsessile, much and irregularly branched, the rays interlocked into a dense felt-like tomentum, this on older plants often abraded by wind and sand; stems to at least 70 cm. long, woody and often much branched; basal leaves none; cauline leaves 1–5 cm. long, more or less linear (2–3 mm. wide), entire or finely and remotely dentate, rounded at the tip, inflorescences loose even before anthesis, the buds large and ellipsoid; sepals 3.5–4.5 mm. long, oblong to elliptic, the lateral sepals saccate, all with a gibbous thickening at the tip; petals 8.5–13 mm. long, chocolate-brown or purplish-brown to olive-green, the claw linear and expanded into a ligulate blade, this elongate but not acuminate; stamens 3.5–5 mm. long; glandular tissue roughly U-shaped on the inside of each single stamen; infructescences loose; pedicels (3.5)4.5–9 mm. long, usually divaricately spreading; siliques 7–10.5 mm. long, ellipsoid to narrowly obovate, terete to slightly compressed; stigmas small and capitate; ovules 5–10 per locule; seeds ca. 1.5 mm. long, oblong to oval and slightly flattened, the testa red-brown to dull orange and smooth.

DISTRIBUTION. Common in the central Australian ranges, especially in the Harts and George Gill ranges; also in the Barrow Range in Western Australia and in central Queensland. Occasionally on sandy soils but most often on stony hillsides and in crevices on rock faces and ledges.

Queensland. 70 miles north of Longreach, *Davidson* in 1953 (BRIU); near Eromanga, *S. T. Blake 11894* (BRI). **Northern Territory.** Tobermory, Nathans Hole paddock, *Chippendale* in 1954 (NSW, NT); Harts Range, 6 miles south of the Police Station, *Chippendale* in 1957 (AD, CANB, NSW, NT, PERTH); sand plain near Barrow Creek, *Gauba* in 1950 (W); Mt. Undoolya, 18 miles east of Alice Springs, *Chippendale* in 1956 (BRI, CANB, NT); Emily Gap, 9 miles e.s.e. Alice Springs, *Nelson 1814* (GH, NT); 1/2 mile s. Ooraminna Rockhole, Ooraminna Range, *J. Must 481* (GH, NT); Yuendumu, *Cleland* in 1951 (A, AD); Haast's Bluff Reserve, *Cleland* in 1957 (AD); George Gill Range and Kathlenn Spring, *Beauglehole 26961* (AD); s.e. side of Mt. Connor, *Beauglehole 22838* (AD). **Western Australia.** Mt. Squires, Barrow Range, *Helms* in 1891 (AD, NSW).

Stenopetalum decipiens owes the epithet ("deceiving") to its similarity to, and frequent confusion with, *S. velutinum*, a species with which it is in part sympatric, and to which name it keys in floristic works dealing with central Australia. Under central Australian conditions, *S. velutinum* seems always to be annual, but *S. decipiens* is clearly perennial and very woody at the base. Plants of the latter (from seed of *Nelson 1814*) grown in the greenhouses of Harvard University were, at three months, clearly woody. Both species are densely pubescent with irregularly branched trichomes, but those of *S. decipiens* are interwoven into a felted tomentum and, with a little care, strips of this tomentum four or five millimeters in length can be peeled from the stems. These interlocked trichomes are especially subject to the abrasive action of wind-blown sand and as a result of such abrasion and excoriation of the thin "bark" mature plants may appear to be quite glabrous. Remnants of the indumentum usually can be found in

leaf axils and stem axils. *Stenopetalum decipiens* has large siliques, on longer pedicels, than does *S. velutinum*, and smooth rather than tuberculate seeds. In both growth form and habitat, *S. decipiens* is much like *Arabidella filifolia*, also a straggling perennial, which often is found on rock faces in the Flinders Ranges of South Australia (Shaw, 1965).

8. **Stenopetalum velutinum** F. Muell. Plants Indig. Col. Vict. 1: 49. 1862. MAP 3.

HOLOTYPE. Victoria or South Australia. Murray Desert, *Mueller* [?] (MEL *10866*).

Plants erect annuals, densely pubescent; trichomes sessile or subsessile, very irregularly branched; stems 1–4(6.5) dm. long, usually branched near the base; basal leaves to ca. 7 cm. long, lanceolate, entire or remotely dentate, withering early and usually lost from fruiting plants; cauline leaves 1–7 cm. long, 1–9 mm. wide, lanceolate to linear, entire or remotely dentate, sessile or shortly petiolate; inflorescences initially dense but elongating at anthesis, buds ellipsoid; sepals 3.5–5.5 mm. long, oblong or elliptic, the lateral saccate, the median cucullate with a callose thickening at the tip; petals 6–21 mm. long, 0.7–1.2 mm. wide, yellow-green to brown, the claw linear and expanded into an elliptic blade, this usually extended into an elongate tip; stamens 3–6 mm. long; glandular tissue a crescentic or rhomboid lobe on each side of each single stamen; infructescences loose, to 20 cm. long; pedicels 2–10 mm. long, slightly spreading or erect; siliques 4.5–6.5(8) mm. long, subglobose to oblong or obovoid; stigmas depressed-capitate and rather fleshy; ovules 10–20 per locule; seeds 1–1.5 mm. long, oblong or elliptic and flattened, orange- or red-brown and tuberculate. $n = 4$, $2n = 8$.

DISTRIBUTION. Widely spread throughout central Australia, also in western Victoria, and in southwestern New South Wales. Although a common species, *S. velutinum* seems never to occur in great abundance.

Queensland. 20 miles west of Miles, *S. T. Blake 5905* (BRI); Armadilla, between the Warrego and Maranoa, *Barton 231* (MEL, NSW); between Stokes Range and Cooper's Creek, *Wheeler* (BM, MEL). **New South Wales.** Brewarrina, *Boorman* in 1903 (BM, NSW); Wanganella, *Officer* in 1903 (NSW). **Victoria.** Nhill, *St. Eloy d'Alton 8* (MEL). **South Australia.** Pedirka, *Ising* in 1932 (AD); gibber plain 43 miles south of Oodnadatta, *Lothian 2183* (AD); Sundown to Granite Downs, *Burbidge & Gray 4591* (CANB); 38 km. east of Tieyon H. S., *Shaw 462* (AD); 11 km. north of Mable Creek, *Shaw 521* (A, AD); Ooldea, *Daisy Bates* in 1920 (AD); Mt. Harriet, *Eichler 17264* (AD, NSW); Piltardi, in Mann Ranges, *Wilson 2541* (AD). **Northern Territory.** Ruby Gorge, Hale River, *Beauglehole 20725* (MEL); Haast's Bluff Reserve, *Cleland* in 1957 (AD); between Mt. Cavanaugh and Victory Downs H. S., *Beauglehole 22767* (MEL); Mt. Olga, *Chippendale* in 1956 (AD, NT). **Western Australia.** West end of Hopkins Lake, *Symon 2323* (ADW); Wingelena Camp, *Wilson 2366* (AD); Mt. Eveline, east of Warburton, *George 3864* (PERTH); Victoria Desert, Camp 54, *Helms* in 1891 (MEL).

Stenopetalum velutinum sometimes is confused with *S. lineare*, the result of that species having been described by De Candolle as glabrous with a subsequent misapplication of the name *S. lineare* var. *canescens*, as in Black's *Flora of South Australia*, to the inland form of *S. lineare*. *Stenopetalum velutinum* has all parts of the plants, even the axes of the inflorescences and the sepals, densely pubescent with appressed trichomes, while plants of *S. lineare*, although often quite densely pubescent towards the base, have the upper parts of the stems glabrous or nearly so. Most closely related to *S. velutinum* and sympatric with it is *S. decipiens* which can be distinguished by the perennial habit and very dense felt-like tomentum.

EXCLUDED SPECIES

STENOPETALUM DRABOIDES Hooker, Icones Plantarum *t. 617*. 1844. Holotype. Western Australia. Swan River, *Drummond* ("Crucif. n. 3") (K) = **Menkea draboides** (Hook.) Bentham.

STENOPETALUM INCISIFOLIUM Hooker f., Icones Plantarum *t. 276*. 1840. Holotype. Tasmania. "Hab. Blackman's River, on the Road to Hobart Town, Van Dieman's Land," *Gunn 644* (K), isotype (GH) = **Hutchinsia procumbens** (L.) Desv.

STENOPETALUM PROCUMBENS Hooker, Icones Plantarum *t. 610*. 1844. Holotype. Western Australia. Swan River, *Drummond 3* (K) = **Menkea australis** Lehm.

STENOPETALUM TRISECTUM Tate, Handb. Flora Extratrop. S. Austral. 17 [in sched.]. 1890. Holotype. South Australia. Innamincka, *McLeod* in 1884 (MEL). The type seems to be a diseased specimen of *S. lineare*.

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ADDENDUM (see comment under *S. lineare*):

In Margaret Willis' *By Their Fruits* (Sydney, 1949) there is a photograph of a specimen of *Helichrysum* collected by Mueller on Lefevre Peninsula on 16 December, 1847, the day after he and his sisters landed. The sheet was annotated by James H. Willis of the National Herbarium of Victoria with the suggestion that this may have been Mueller's first botanical specimen from Australia. However, the comment on the label of the *Stenopetalum* leaves, I think, no doubt that it was crucifer rather than composite which first attracted the Baron's botanical attention.

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A REVISION OF THE NEOTROPICAL GENUS LISIANTHIUS (GENTIANACEAE)

RICHARD E. WEAVER, JR.[1]

THE GENUS *Lisianthius* as here interpreted comprises 27 species and 2 varieties of woody or semiwoody Gentianaceae distributed throughout the Greater Antilles and continental America, from south-central Mexico to northwestern Colombia. Although the plants are frequently found on roadside banks, and the flowers are usually large and showy, the genus has been rather poorly collected.

The genus was last monographed by Perkins (1902) but that treatment is little more than a checklist with keys to only a fraction of the species now recognized. The present treatment is based upon examination of approximately 1500 specimens, nearly one third of which were especially collected for it. In addition 20 of the 27 species were studied in the field, at which time seeds and preserved material for cytological and anatomical investigation were obtained, and 10 species were grown in the greenhouse.

HISTORY OF THE GENUS

As indicated by the inordinately long list of "excluded names" at the end of this paper, *Lisianthius* has been broadly construed by many authors in the past. In addition, a number of orthographic variants of the name have been used. The genus, as *Lisianthius*, was first defined by Patrick

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Browne (1756). He described two species, both from Jamaica: *Lisianthius erectus, foliis lanceolatis floribus singularibus terminalibus*; and *Lisianthius foliis cordato-acuminatis, petiolis brevibus, floribus terminalibus quandoque geminatis*. Browne placed the generic description following that of the first species, as was his custom (W. T. Stearn, *in litt.*). Linnaeus (1767), in taking up Browne's genus, changed the spelling of the name to "*Lisianthus*." He assigned a binomial, *L. longifolius*, to Browne's first species, and *L. cordifolius*, to the second. Linnaeus's spelling of the name has been the one most commonly used. In fact, Rothmaler (Fedde, Repert. Sp. Nov. 53: 178. 1944.) proposed conservation of *Lisianthus* L. over *Lisianthius* P. Browne. However, the proposal was rejected (Taxon 3: 242. 1954). Only Kuntze (1891) and more recently Weaver (1969, 1970) and Robyns and Nilsson (1970) have used the correct and original spelling "*Lisianthius*."

Aublet (1775) described four species from French Guiana, using the name *Lisyanthus*. Aublet's plants are allied to but not congeneric with *Lisianthius* P. Browne, according to the present interpretation. It is difficult to believe that Aublet meant to establish a new genus, in view of the close relationship of his plants to *Lisianthius* P. Browne and the nearly identical spelling of the names. Yet, according to W. T. Stearn (*in litt.*), when Aublet (*loc. cit.*) furnished a detailed generic description, as he did in the case of *Lisyanthus*, his intent was to establish a new genus. For previously established genera, he merely cited the generic name.

If *Lisyanthus* Aubl. is indeed to be interpreted as a genus distinct from *Lisianthius* P. Browne, under the present International Code the name must be treated as an orthographic variant of *Lisianthius* P. Browne and therefore a later homonym (Art. 75) to be rejected (Art. 64).

The younger Linnaeus (1781) added two species to his father's *Lisianthus*: *L. chelonoides* and *L. glaber*, neither of which are referable to *Lisianthius* P. Browne. He cited "*Lisianthus alatus* Aubl." as a synonym of *L. chelonoides*, evidently considering *Lisyanthus* Aubl. as merely an orthographic variant of *Lisianthus* L.

Sprengel (1825) included, in what he called "*Lisianthus* P. Browne," species described by Linnaeus (1767), Aublet (1775), Linnaeus filius (1781), Swartz (1788), Kunth (1818), and others. Most of these are not referable to *Lisianthius* P. Browne as interpreted here.

Grisebach (1839) gave to *Lisianthius* P. Browne the new but nomenclaturally superfluous name *Leianthus* and divided the genus into two sections, LISIANTHIUS (P. Browne) Griseb. and OMPHALOSTIGMA. In addition he accepted *Lisyanthus* Aubl., which he divided into five sections: MACROCARPAEA, CHORIOPHYLLUM, CHELONANTHUS, HELIA (Mart.) Griseb., and CALOLISYANTHUS. Later Grisebach (1845), while maintaining *Leianthus*, elevated *Leianthus* sect. OMPHALOSTIGMA to generic rank as *Petasostylis*. At the same time he used the name *Lisianthus*, attributed to Aublet (1775), for his earlier *Lisyanthus*, but left the content of the genus essentially unchanged.

Bentham (1876) maintained *Leianthus* in the sense of Grisebach

(1839), including *Petasostylis* as a synonym, and *Lisianthus*, which he attributed to Aublet (1775). While accepting the sections of Grisebach (*loc. cit.*) he added three new sections to the latter genus: SYMBOLANTHUS (G. Don) Benth. & Hook. including *Leiothamnus* Griseb., ADENOLISIANTHUS (Progel) Benth. & Hook., and IRLBACHIA (Mart.) Benth. & Hook.

Kuntze (1891) correctly applied *Lisianthius* P. Browne and treated *Lisianthus* L. and *Leianthus* Griseb. as synonyms. Doubting that Aublet (1775) meant *Lisyanthus* to be a new genus, Kuntze adopted the name *Helia* Mart. for *Lisyanthus* (*Lisianthus*) Aubl. *sensu* Grisebach (1839, 1845) and Bentham (1876).

Gilg (1895), whose system has been employed by most recent authors, continued the taxonomic separation made by his immediate predecessors, but used the name *Lisianthus* L. for the plants here referred to *Lisianthius* P. Browne. Gilg employed a rather narrow generic concept based for the most part on pollen morphology. He elevated to generic status all of the groups which Bentham (1876) had previously treated as sections of "*Lisianthus* Aubl."

INTERGENERIC RELATIONSHIPS

In Gilg's (1895) treatment of the family *Lisianthius* (as *Lisianthus*) was associated with seven other genera, most of them small, and all but one, *Tachiadenus* Griseb., restricted to the New World, in the tribe Gentianeae subtribe Tachiinae. Gilg's fundamental taxonomy of the family was based almost entirely on the morphology of the pollen grain. As previously pointed out (Weaver, 1969), Gilg's treatment is unsatisfactory in a number of respects.

Anatomically the Tachiinae resemble the plants in Gilg's tribe Helieae more than they do those in other subtribes of the Gentianeae. Perrot (1898) reported that only the Helieae and Gentianeae-Tachiinae are characterized by having mechanical elements in the cortical area of the stem. Lindsey (1937, 1940) reported that the anatomical features of the Helieae are strikingly similar to those of the Tachiinae, but are more advanced. The two groups of genera are characterized by the nearly constant occurrence of glandular tissue at the base of the ovary, a character found only sporadically in other groups of the family. *Lisianthius* is similar to the Helieae in having fused calyx-lateral traces, found in none of the other generic groups. *Macrocarpaea glabra* (L.f.) Gilg and *Zonanthus cubensis* Griseb., both placed by Gilg in the Tachiinae, do not have fused calyx-laterals, but in other respects the flowers of these species are anatomically identical to those of the Helieae (Lindsey, 1937). Lindsey, in fact suggested, that although the Helieae and the Tachiinae are sufficiently different to be placed in distinct groups "of some grade," the similarities are such that the Helieae be best reduced to subtribal status in the Gentianeae.

According to Gilg (1895) the Helieae are unique in the family in possessing pollen that is held in tetrads or polyads. Since *Macrocarpaea*

glabra and *Zonanthus cubensis* have single pollen grains but are anatomically nearly identical to Gilg's Helieae, the value of pollen in tetrads as a character for delimiting a group as large as a tribe seems questionable here.

As explained earlier, *Lisianthius* has been broadly construed in the past, and the name, usually as *Lisianthus* or *Lisyanthus*, has been applied to a rather diverse group of plants. Nilsson (1970) recently surveyed the pollen morphology of these lisianthioid gentians, and his results are at variance with those of Gilg. He reported that, while the pollen types in *Lisianthius* (as delimited in this study), *Macrocarpaea* (Griseb.) Gilg, *Rusbyanthus* Gilg, and several anomalous species are distinctive, the pollen grains of *Adenolisianthus* (Prog.) Gilg, *Calolisianthus* (Griseb.) Gilg, *Chelonanthus* (Griseb.) Gilg, *Helia* Mart., *Irlbachia* Mart., *Lehmaniella* Gilg, *Pagaea* Griseb., *Purdieanthus* Gilg, and *Symbolanthus* G. Don all have approximately "the same basic morphology and some even have features which are transitional within the range of variation of pollen types in the genera."

The taxonomy of these lisianthioid gentians is in a state of chaos. *Macrocarpaea* is the only genus of any size monographed during this century. The genus, as treated by Ewan (1948) is apparently heterogeneous and hence unnatural. Nilsson (1968) found three pollen types in *Macrocarpaea*: a distinctive one; a type identical to that of *Rusbyanthus*, a monotypic genus placed by Gilg in a separate tribe between the Gentianeae and the Helieae; and a final type, with pollen in tetrads, similar to that found in *Chelonanthus*, a genus placed by Gilg in the Helieae. Those species of *Macrocarpaea* with *Rusbyanthus*-type pollen do not deviate significantly in other respects from others in the genus. Neither for that matter does *Rusbyanthus cinchoniifolius* Gilg, and the two genera should probably be combined. Those species of *Macrocarpaea* with pollen in tetrads resemble *Chelonanthus* morphologically, and probably should be combined with it.

The remaining lisianthioid genera, all placed by Gilg in the tribe Helieae, are in general difficult to characterize morphologically. *Lagenanthus* Gilg, *Lehmaniella*, and *Purdieanthus* differ from the remaining genera in having tubular corollas, but, contrary to Ewan's (1948b, 1952) findings, I have been unable to recognize reliable morphological criteria for separating them. *Helia* is distinctive in having a salverform corolla, but in other respects it closely resembles *Chelonanthus*. Intergradation between *Adenolisianthus*, *Calolisianthus*, *Chelonanthus*, *Irlbachia*, and *Pagaea* completely obscures generic boundaries.

Several species are anomalous in both pollen and gross morphology and appear not to fit into any of the existing genera. These include *Irlbachia caerulescens* (Aubl.) Gilg, *Calolisianthus imthurnianus* (Oliver) Gleason, *Lisianthus chimantensis* Steyerm. & Maguire, and *Calolisianthus frigidus*. The last species, however, according to Nilsson (1970) has pollen approaching that of *Symbolanthus*.

Study of this entire group of gentians has been hampered not only by the pitifully small number of existing specimens but also by the

wretched condition of many of them. Cytological studies may prove of considerable taxonomic value as indicated by the few chromosome counts reported by Weaver (1969). At any rate these plants are in need of concentrated study. Nilsson's pollen work is a good starting point. However, the study, when and if it is made, must be a more comprehensive one than that of Gilg. Gilg's work shows quite well the confusion that often results from reliance on a single character in the classification of a large group of plants. A comprehensive study of the lisianthioid gentians is beyond the scope of this paper and no formal taxonomic decisions concerning them will be made at present. Instead, the following key has been prepared as an aid in distinguishing, wherever possible, the lisianthioid gentians as they now stand (*Irlbachia caerulescens*, *Lisianthus chimantensis*, and *Calolisianthus imthurnianus* are not included; those species of *Macrocarpaea* with pollen in tetrads key out under *Chelonanthus*).

KEY TO THE GENERA OF LISIANTHIOID GENTIANS

1. Stigmas capitate or peltate, indistinctly bilobed, the lobes never linear or flattened; ovary unilocular or weakly bilocular, the placentae barely projecting into the lumen of the ovary, never inrolled; old placentae visible as whitish, erose bands along the margins of the dehisced capsules adjacent to the suture; corolla tube with usually conspicuous bundles of metaxylary fibers; main stem terete. ..... *Lisianthius*.
1. Stigmas bifurcate, the lobes linear or flattened; ovary unilocular or bilocular, the placentae conspicuously inrolled, projecting strongly into the lumen of the ovary and nearly filling it; old placentae not visible on the mature capsules, the margins adjacent to the sutures smooth; corolla tube without bundles of metaxylary fibers; main stem usually 4-angled.
   2. Pollen grains single; inflorescences branched systems of apparently simple dichasia, the divisions subtended by conspicuous foliar bracts; foliage leaves with many pairs of principal lateral veins. ..... *Macrocarpaea, Rusbyanthus*.
   2. Pollen grains in tetrads or polyads; inflorescence an apparently simple dichasium or much more commonly a compound dichasium, this once or twice bifurcately branched, the lateral divisions often secund or complanate and appearing racemose, the divisions never subtended by foliar bracts; foliage leaves with 2–3 pairs of principal lateral veins.
      3. Bases of the stamens joined by a carnose cylinder of tissue, with triangular teeth opposite the stamens; connectives of the anthers long exserted; inflorescences sessile or nearly so; flowers usually more than 6 cm. long, the corolla funnelform. ..... *Symbolanthus*.
      3. Bases of the stamens connected by a carnose cylinder of tissue or not, but the cylinder never with triangular teeth; connectives of the anthers included or short-exserted; inflorescences long-pedunculate; flowers usually campanulate, or rarely tubular, salverform, or funnelform.
         4. Corolla tubular. ..... *Lagenanthus, Lehmaniella, Purdieanthus*.
         4. Corolla campanulate, rarely salverform or funnelform.
            5. Corolla salverform; foliage leaves concentrated in the lower half of the stem. ..... *Helia*.

5. Corolla campanulate, rarely funnelform; foliage leaves evenly distributed along the stem.
   6. Leaves usually palminerved, sessile, coriaceous or subcoriaceous, rarely penninerved; lobes of the stigma much broader than the style; inflorescence an apparently simple or a compound dichasium, the lateral branches never appearing racemose, or often reduced to a single flower. . . . . *Calolisianthus.*
   6. Leaves, at least the lower ones, penninerved and petiolate, membranaceous or very rarely coriaceous; lobes of the stigma usually but barely broader than the style; inflorescence a once or twice bifurcately branched dichasium, the ultimate branches usually secund or complanate and appearing racemose, or very rarely the inflorescences reduced to a single, terminal flower.
      7. Ultimate branches of the inflorescences equal, usually secund or complanate; style conspicuously longer than the ovary; anthers longer than broad; corolla often gibbous; pollen in tetrads or polyads; coarse annuals or perennials. . . . . *Chelonanthus, Adenolisianthus, Macrocarpaea arborea, M. cerronis, M. quelchii, M. salicifolia.*
      7. Ultimate branches of the inflorescences often unequal, seldom secund; style usually shorter than the ovary or equalling it; anthers usually about as broad as long; corolla never gibbous; pollen in polyads; annuals. . . . . *Pagaea, Irlbachia.*

Lisianthius is easily separated from the other lisianthioid genera by the characters outlined in the key. The capitate or peltate, indistinctly lobed stigmas, the weakly projecting placentae, the presence of floral fibers, as well as the characteristic pollen morphology mentioned earlier, clearly set it apart as a distinct genus. Therefore I would disagree with Steyermark (1953) who argued for the inclusion of several of the lisianthioid genera, e.g. *Chelonanthus*, *Calolisianthus*, *Irlbachia*, and *Pagaea*, within *Lisianthius*.

MORPHOLOGY

Habit. The species of *Lisianthius* have been described as annual or perennial herbs, shrubs, or trees. *Lisianthius capitatus*, for example, is referred to as an herb by some collectors and a slender tree by others. Field observations, coupled with herbarium studies and observations of cultivated plants have led me to conclude that most of the species are perennials, although some of them may be rather short-lived.

Plants of sect. LISIANTHIUS subsect. HERBACEI appear to be mostly perennial, suffrutescent herbs. Only the primary roots and the basal 1 dm. of stem are distinctly woody. In the field, plants usually have both a green flowering shoot and a dead shoot with old empty capsules present at the same time. Cultivated plants of *L. nigrescens* die back to the base

after flowering and eventually new shoots are produced from the lower nodes. All plants of the subsection are monopodial. The branching is excurrent and generally opposite, and all of the shoots are determinate.

The species of section OMPHALOSTIGMA are similar in aspect and growth form to those of sect. LISIANTHIUS subsect. HERBACEI; they are coarse monopodial herbs with opposite, excurrent branching. *Lisianthius meianthus*, however, is definitely an annual. The only population of this species seen in the field, in eastern Guatemala, was made up of old dead individuals and young vegetative ones. Living and dead shoots were never present on the same plant.

The plants of sect. LISIANTHIUS subsect. FRUTICOSI are all perennials. Most species are subshrubs. Even though the aërial portions of these plants persist more than one season, they are not distinctly woody except at the base. Many of the species flower the first or second year from seed, when they are still predominantly herbaceous. *Lisianthius exsertus*, *L. jefensis*, *L. skinneri*, and sometimes *L. peduncularis* are true shrubs, while *L. capitatus* and *L. umbellatus* become slender trees with stems to 6 meters tall and 8 cm. in diameter.

The plants of sect. LISIANTHIUS subsect. FRUTICOSI are generally not monopodial; the branching is opposite or alternate and is not excurrent. These typically have a single main trunk which is branched above. However, in most species, certain individuals may be entirely unbranched and spindly, resembling herbs. The main shoots are indeterminate, and the inflorescences are borne on determinate, lateral shoots.

The genus may be divided into two artificial groups on the basis of habit. The species of sect. OMPHALOSTIGMA and sect. LISIANTHIUS subsect. HERBACEI are annual or perennial suffrutescent herbs with determinate main axes. The species of sect. LISIANTHIUS subsect. FRUTICOSI are subshrubs, shrubs, or slender trees with indeterminate main axes. This difference in habit is one of the primary characters used here to divide sect. LISIANTHIUS into two subsections. Unfortunately, this character is often difficult to interpret from herbarium specimens. Most species, even the herbaceous ones, are rather tall and coarse and since it may be impossible to fit an entire plant on an herbarium sheet, often only lateral branches are collected. These are determinate in both subsections of sect. LISIANTHIUS and may easily be mistaken for the main axes.

Indument. Most species of *Lisianthius* lack an indument of any sort. However, a very fine pubescence is present in *L. cordifolius* and *L. meianthus*, and in some collections of *L. glandulosus*, *L. longifolius*, and *L. saponarioides*. Although the pubescence may be rather dense, only in *L. cordifolius* and *L. longifolius* is it readily evident without magnification. The individual hairs (or excrescences) are unicellular, 1 mm. or (often considerably) less in length, and the pubescence is best described by the terms "puberulous" or "spiculate."

Stems. Decurrent from the leaf bases on opposite sides of the her-

baceous portions of the stems are pairs of raised parallel ridges, which run the length of each internode and are usually inconspicuous without magnification. The ridges of each pair are generally close together, appearing as one. In some species, however, the ridges of each pair are widely separated, the stem then appearing indistinctly 4-angled. The angles may be expanded into narrow, scarious wings, which in *L. cuspidatus* are minutely serrulate.

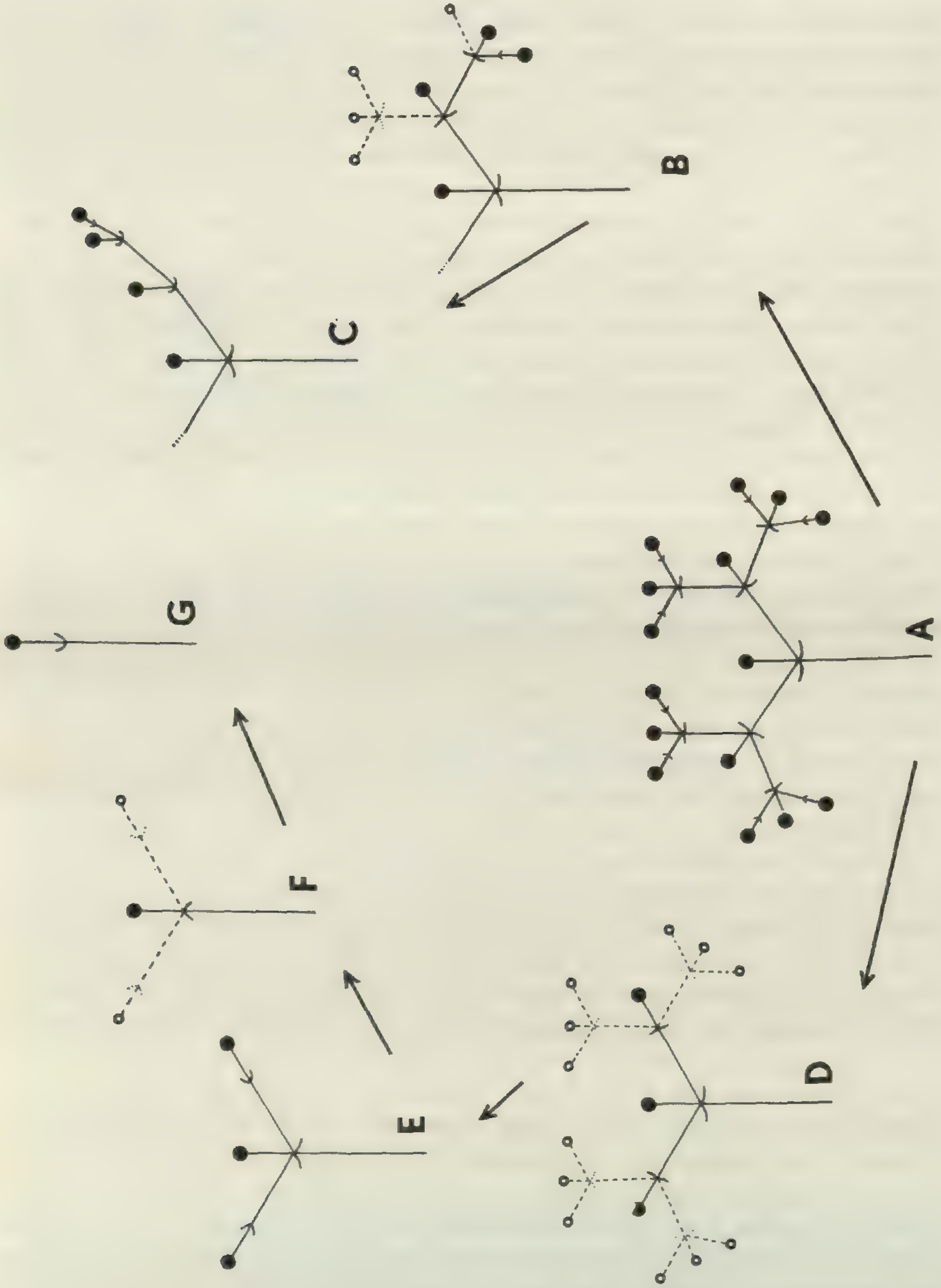
Leaves. The genus is also easily divided into two artificial groups on the basis of whether or not the foliage leaves are truly sessile. The species of sect. LISIANTHIUS subsect. HERBACEI are characterized by sessile, usually clasping foliage leaves. In these species the lamina of the blade is confluent with the basal sheath, and the petiole is entirely lacking at least in the lower leaves; the upper leaves may be short-petiolate. In the species of sect. OMPHALOSTIGMA and subsect. FRUTICOSI of sect. LISIANTHIUS, the leaves are narrowed to a petiole which may be winged and very short, causing the leaves to appear subsessile.

The leaves on the determinate lateral branches of all species, as well as those leaves subtending the lateral branches in sect. OMPHALOSTIGMA and sect. LISIANTHIUS subsect. HERBACEI, are smaller and of different shape than the foliage leaves. When the foliage leaves are elliptic, obovate, or oblanceolate, the upper leaves and those on the lateral branches are ovate or lanceolate; when the foliage leaves are ovate or lanceolate, the upper leaves and those on the lateral branches are lanceolate or linear. In sect. OMPHALOSTIGMA and subsect. HERBACEI of sect. LISIANTHIUS the transition is gradual. In subsect. FRUTICOSI of sect. LISIANTHIUS the transition is abrupt; the difference between the two types of leaves is striking, especially in such species as *L. capitatus*, *L. cordifolius*, and *L. umbellatus*.

The presence of two types of leaves on one plant makes the interpretation of leaf size and shape rather difficult, especially when only a lateral branch has been preserved. In this study "foliage leaves" refers to those leaves on the main shoots of plants of sect. LISIANTHIUS subsect. FRUTICOSI, or those leaves on the main shoot which do not subtend a lateral shoot in sect. OMPHALOSTIGMA and subsect. HERBACEI of sect. LISIANTHIUS.

The leaves of sect. LISIANTHIUS subsect. FRUTICOSI are evergreen, but after a period of one to two years they absciss. Thus, at least in older plants of this subsection, the lower portion of the stem lacks leaves. The leaves of plants in the genus are opposite, the bases of the leaf pair being joined by a green or somewhat scarious, truncated sheath. The sheaths persist after the leaves have abscissed, giving a jointed appearance to the stem. Williams (1968: p. 410) suggested that these sheaths are perhaps homologous with the interpetiolar stipules of the Rubiaceae.

Inflorescences. The inflorescences of *Lisianthius* are rather difficult to interpret, and as a result have been variously described as "cymose,"


A
B
C
D
E
F
G

"thyrsoid," or "dichasial." According to my interpretation, the inflorescences in the genus are basically compound dichasia. There have been, however, many modifications on the basic scheme. The dichasia may be 1 to 5 times compound, or they may be reduced (1) to the point where they appear simple, or (2) to single flowers. The subunits of the dichasia may be 3-flowered, or one flower in each may abort, so that the lateral branches appear scorpioid. The various modifications of the dichasium, as found in *Lisianthius*, with a possible sequence of these modifications, are illustrated in FIGURE 1.

FIGURE 1-A represents a normal (twice-) compound dichasium, the basic type found in the species of sect. OMPHALOSTIGMA and most of those in sect. LISIANTHIUS subsect. HERBACEI. This type of dichasium is found in many gentianaceous genera, including *Centaurium*, *Curtia*, *Sabatia*, and *Schultesia*, and is probably the generalized one in the family. Each of the subunits is subtended by a pair of bracts, the lowermost often foliaceous, the upper ones becoming scarious. The lateral pedicels of each of the ultimate subunits are subtended by a pair of scarious bracteoles, in the axils of which aborted buds are frequently found, indicating that the lateral flowers themselves represent reduced subunits.

From Type 1-A, the modifications have probably proceeded in two directions. FIGURE 1-C represents the type of modified compound dichasium found typically in *Lisianthius brevidentatus* and not infrequently in the remaining species, except for *L. cuspidatus*, of sect. LISIANTHIUS subsect. HERBACEI, as well as *L. seemanii* (sect. LISIANTHIUS subsect. FRUTICOSI). This type, in which the lateral branches appear scorpioid, is easily derived from Type 1-A, as shown in FIGURE 1-B, by the loss of branches or flowers on one side (often but not always the same side) of each trichotomy.

Although it may at first appear to be a simple dichasium, FIGURE 1-E actually represents a reduced compound type. The lateral axes are dichasial branches terminated by a solitary, pedicellate flower. That they are not merely simple, bracteolate pedicels is borne out by two observations: (1) aborted buds are frequently found in the axils of the bracteoles; and (2) the morphology of the axis is different above and below the bracteoles in that the raised parallel ridges mentioned before are absent above them. Type 1-E is the basic type of dichasium found in most of the species of sect. LISIANTHIUS subsect. FRUTICOSI. In addition this type is occasionally found in the other species of sect. LISIANTHIUS subsect. HERBACEI and regularly in *L. cuspidatus*. It is easily derived from Type 1-A, as shown in FIGURE 1-D, by loss of the upper subunits. In this study, Type 1-E will be referred to as an "apparently simple" dichasium.

FIGURE 1-G represents the ultimate in the reduction of the dichasium as found in *Lisianthius*. The lateral branches of Type 1-E, as shown in

FIGURE 1 (opposite). The probable sequence in the evolution of the dichasium in *Lisianthius*. See text above for explanation.

FIGURE 1-F, have been lost by reduction and a single flower remains. This type is found typically in *L. axillaris* and not infrequently in most of the other species of sect. LISIANTHIUS subsect. FRUTICOSI. Types 1-A and 1-C then, are the ones typical of most species of sect. OMPHALOSTIGMA and sect. LISIANTHIUS subsect. HERBACEI. Types 1-E and 1-G are the ones typical of most of the species of subsect. FRUTICOSI of sect. LISIANTHIUS.

The various arrangements of the inflorescences in the genus, with one possible sequence in their evolution, are shown schematically in FIGURE 2. Types 2-A, 2-B, and 2-C are similar, except for the modifications in the dichasia which were discussed earlier. In these three types, the dichasia are terminal and axillary on the primary and secondary shoots, all of which are determinate. The secondary shoots are frequently leafy below the first division and are basically similar to the upper portion of the primary shoot. In some species, such as *Lisianthius brevidentatus* (arrangement as in FIGURE 2-C) and *L. saponarioides* (arrangement as in FIGURE 2-A) the dichasia are frequently sessile or nearly so, and the upper internodes very short, so that the inflorescences appear compacted. Types 2-A to 2-C are characteristic of the species in sect. OMPHALOSTIGMA and subsect. HERBACEI of sect. LISIANTHIUS.

The remaining types shown in FIGURE 2 are characteristic of the species in sect. LISIANTHIUS subsect. FRUTICOSI. In these species the primary axes are indeterminate. The dichasia are axillary or, more commonly, terminal and axillary on determinate lateral shoots, which in this study will be referred to as "flowering branches."

Except for *Lisianthius* and a few closely related genera, the Gentianaceae are herbaceous with terminal inflorescences. The condition in sect. LISIANTHIUS subsect. FRUTICOSI, in which the plants are woody with indeterminate axes, must certainly be a derived one. Since the species of subsect. FRUTICOSI of sect. LISIANTHIUS are characterized almost entirely by having apparently simple dichasia, the evolution from determinate to indeterminate main axes has probably been through the type represented by FIGURE 2-B.

Flowering branches are probably homologous with the lower lateral shoots of Types 2-A to 2-C. The basic type is shown in FIGURE 2-D. The branching is opposite and each division is terminated by an apparently simple dichasium. One to three pairs of reduced leaves are present below the lowermost trichotomy, but rarely are any present above. Rather, the upper divisions are subtended by somewhat foliaceous or scarious bracts. This type is found occasionally in most species of sect. LISIANTHIUS subsect. FRUTICOSI and regularly in *L. latifolius* and the *L. skinneri* complex.

Specialization has progressed from Type 2-D in two directions. Through Types 2-E (*L. longifolius*) to 2-F (*L. longifolius*) and 2-G (*L. cordifolius*) the flowering branches become more complex and freely branched, with reduced leaves found above the first division and on the secondary axes. The dichasia are mostly reduced to single flowers. The branching is op-

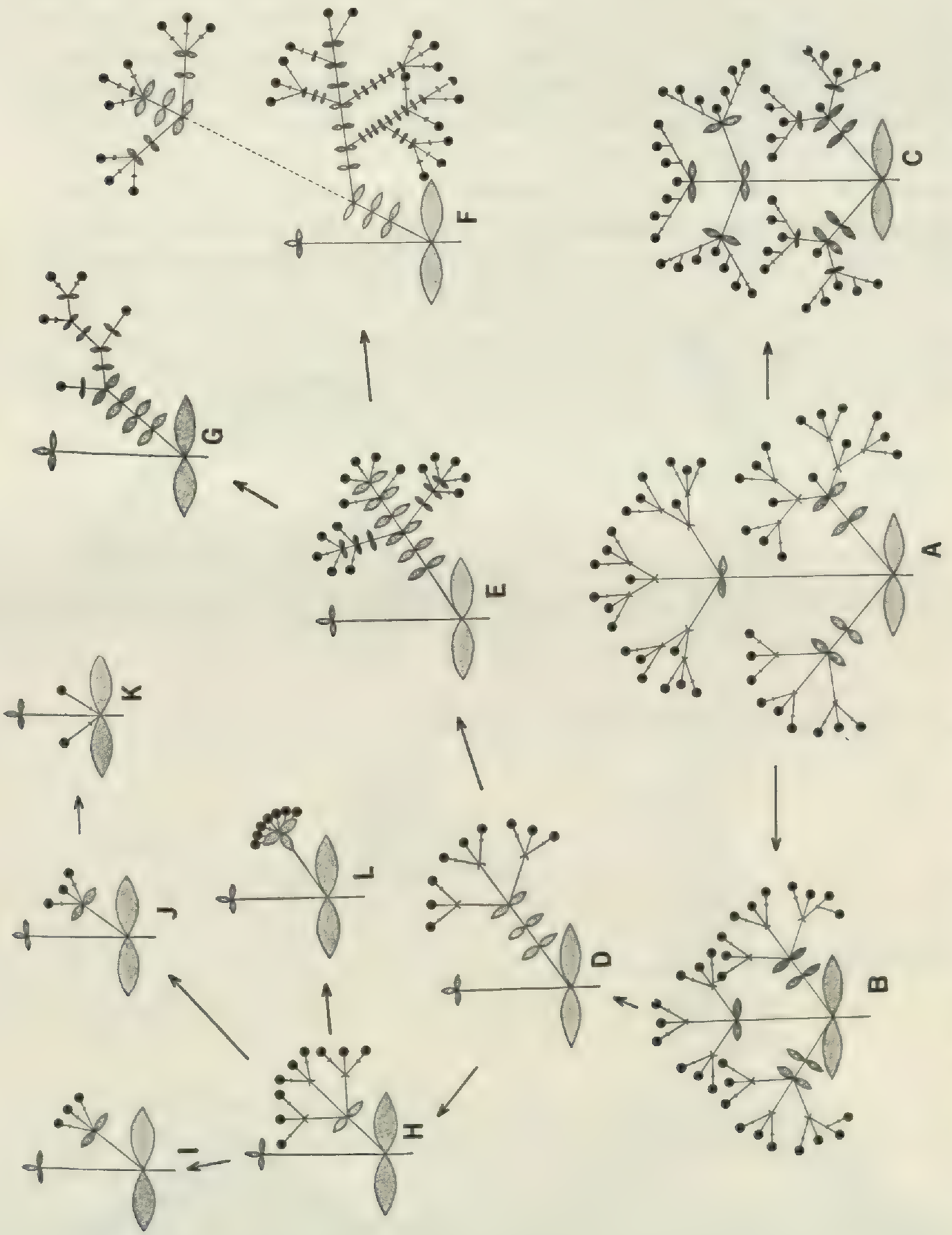


FIGURE 2. The arrangement of the inflorescences in *Lisianthius* and the probable sequence in the evolution of this arrangement. See text for explanation.

posite, alternate or bifurcate in Types 2-E and 2-F, and nearly always bifurcate in Type 2-G.

From Type 2-D through Types 2-H to 2-K, the flowering branches become simpler. The leaves are reduced in number to a single pair subtending the lowermost division, or, are lacking. The branching is reduced, resulting in (FIGURE 2-I) three flowers, each a reduced dichasium, an apparently simple dichasium (FIGURE 2-J), or, ultimately, a single flower (FIGURE 2-K). Type 2-H is typical in all of the species of series *Longifolii* (except for *L. axillaris*) and series *Exserti* of sect. LISIANTHIUS subsect. FRUTICOSI. Types 2-I to 2-K are found occasionally in the above-mentioned series, and Type 2-K is typical in *L. axillaris*.

Type 2-L, which is characteristic of the two species in sect. LISIANTHIUS subsect. FRUTICOSI series *Umbellati*, closely resembles Type 2-H

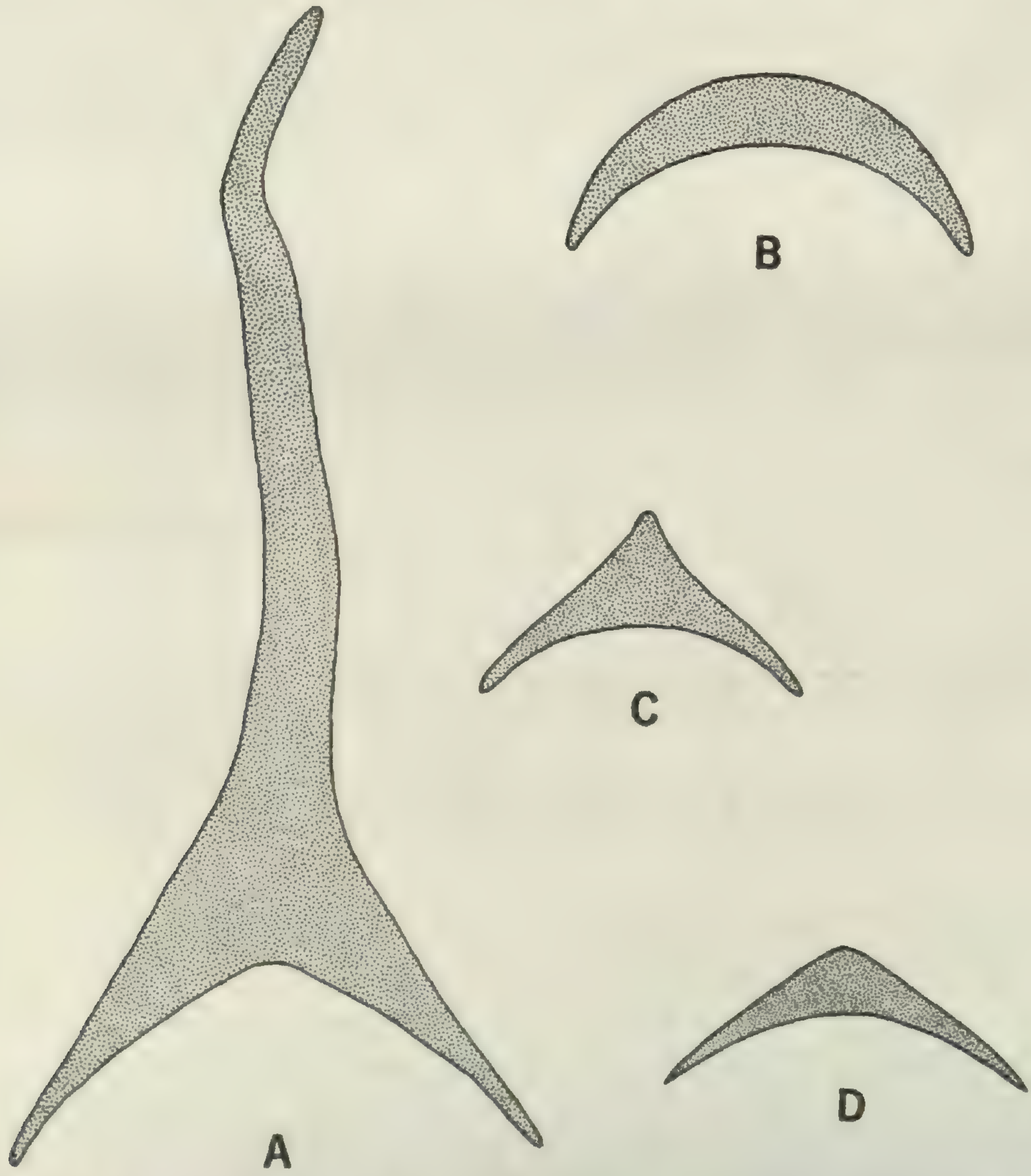


FIGURE 3. Cross-sections of the calyx lobes of representative *Lisianthius* species. A. *L. longifolius*, lobes alate; B. *L. viscidiflorus*, lobes completely ecarinate; C. *L. cordifolius*, lobes carinate; D. *L. auratus*, lobes ridged.

when dissected, and is clearly derived from it. The internodes above the lowermost division and the stalks and branches of the dichasia are greatly shortened, the whole affair resembling a capitulum or an umbel. The bracts subtending the two lowest divisions are large and foliaceous and appear involucrate.

Flowers. In most species the calyx lobes are carinate abaxially to some degree. The width of the keel varies from species to species, from a slight, almost imperceptible ridge along the midline, to a conspicuous wing 4 mm. broad. In a few species the lobes are completely ecarinate. The terms used in this study to describe the abaxial surface of the calyx lobes are defined below. Lobes, drawn in cross section, representing each of the types are shown in FIGURE 3.

Ecarinate: the abaxial surface of the lobes uniformly convex (3-B).

Ridged: the lobes thickened along the midline, the sides in cross section straight or slightly concave (3-D).

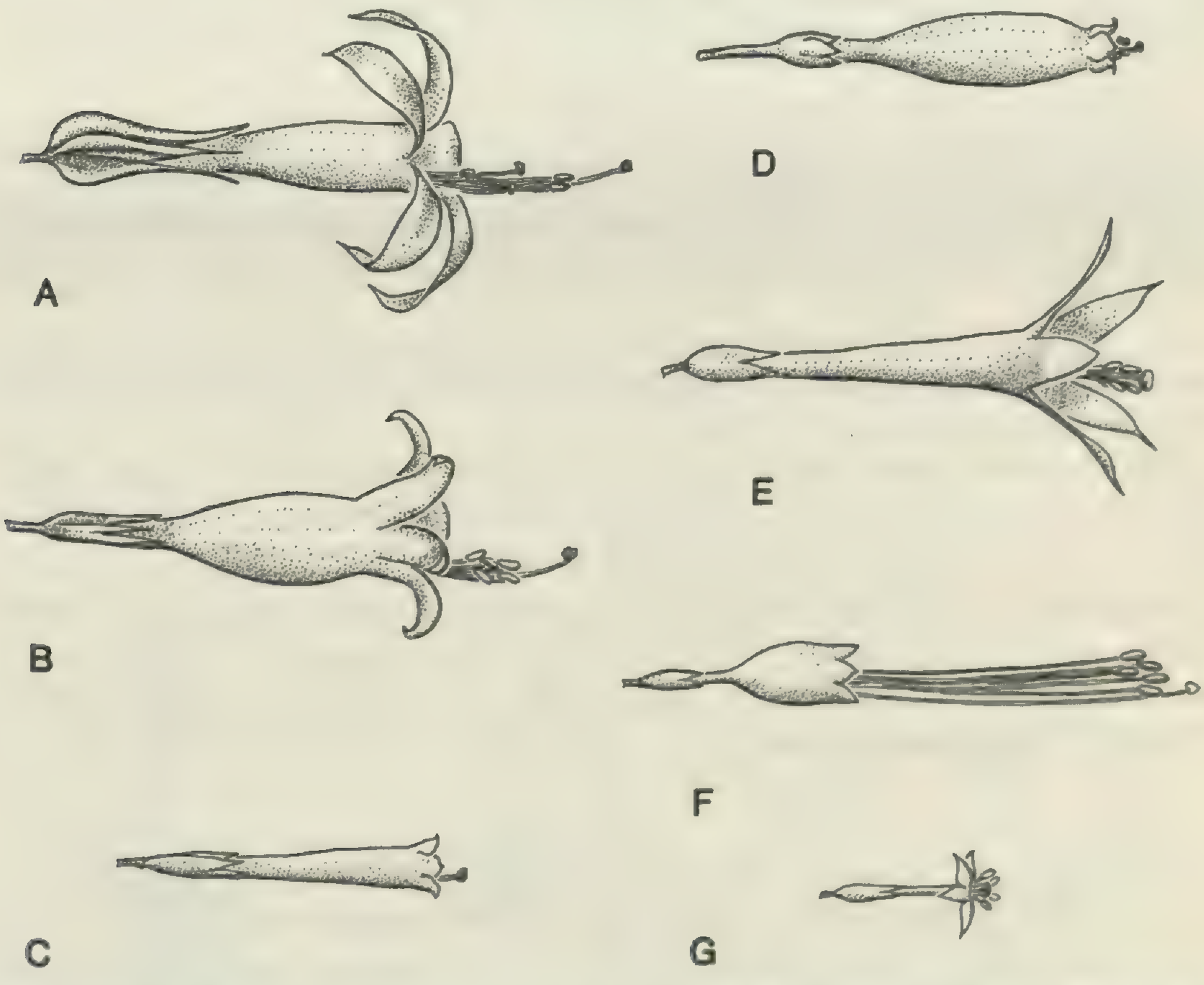


FIGURE 4. Flowers of representative species of *Lisianthius*, showing the various corolla shapes and the posture of the corolla lobes, × 1. A. *L. longifolius*, corolla tubular-funnelform, lobes recurved; B. *L. adamsii*, corolla tubular-funnelform, inflated, lobes somewhat recurved; C. *L. brevidentatus*, corolla tubular, lobes spreading; D. *L. skinneri*, corolla tubular, inflated, lobes recurved at the tips; E. *L. nigrescens*, corolla funnelform, lobes spreading; F. *L. exsertus*, corolla tubular-campanulate, lobes erect; G. *L. saponarioides*, corolla salverform, lobes flaring.

Carinate: the lobes strongly thickened along the midline, the thickened portion slightly projecting; in cross section the sides strongly concave (3-C).

Alate: the thickened portion along the midline of the lobes expanded into a thin, flat, membranous and strongly projecting wing (3-A).

Although the last three calyx-lobe types intergrade from species to species, they are generally constant in a given species.

The structure of the corolla of all the species is basically the same. However, the proportions of the sectors vary, resulting sometimes in strikingly different shapes. The basal sector of the corolla tube, usually the lower third or sometimes the lower half, that portion enclosing the ovary and in turn enclosed by the calyx, is constricted into a narrow tube with parallel sides. The stamens are inserted near the distal end of this constriction. Above the insertion of the stamens, the corolla tube expands, often abruptly but sometimes gradually, into a somewhat broader tube which is terminated in the limb. The terms used in this study to describe the various corolla shapes are defined below.

Tubular: the upper, expanded portion of the tube long and relatively narrow, with more or less parallel sides or somewhat inflated; the limb short and erect or gradually spreading (FIGURES 4-C, 4-D).

Tubular-funnelform: differing from the tubular only in that the limb is relatively long and recurved (FIGURES 4-A, 4-B).

Funnelform: the upper expanded portion of the tube long and narrow, tapering gradually to the throat; the limb relatively long and gradually spreading (FIGURE 4-E).

Tubular-campanulate: the upper, expanded portion of the tube short and broad, tapering slightly to the throat; the limb short and erect or gradually spreading (FIGURE 4-F).

Salverform: the tube narrowly constricted for nearly the entire length, with the sides more or less parallel; the upper, expanded portion of the tube nearly obsolete, and the limb at right angles to the tube (FIGURE 4-G).

Pressing and drying frequently alter the shape of the corolla. The lower, constricted portion of the tube is greatly exaggerated in dried specimens, and the posture of the limb, erect, spreading or recurved, is frequently difficult to interpret.

The corollas of all species are marcescent to some degree, that is the corolla withers after anthesis but does not absciss for some time. In some species, particularly those of sect. LISIANTHIUS subsect. HERBACEI, the corolla may persist for months after the capsule matures and the seeds are shed. In most species of sect. LISIANTHIUS, however, the corolla does absciss before the capsule matures. The degree to which the corolla persists appears to be correlated with the amount of sclerification of the vascular traces to the corolla. Those species in which the fibrous bundles are most conspicuous and best developed are the species in which the corolla persists on the mature capsules.

The stamens are inserted on the corolla tube ca. 1/2–1/3 of the distance

from the base to the apex in sect. LISIANTHIUS or just below the apex in sect. OMPHALOSTIGMA. In dried flowers, the point at which the filaments become free from the corolla is usually visible externally as a slight swelling on the lower constricted portion of the corolla tube.

In sect. OMPHALOSTIGMA the filaments are of equal length in a given flower; in sect. LISIANTHIUS the filaments are of unequal length in a given flower, usually two short, two of intermediate length, and one long. From observations of greenhouse plants, it appears that the filaments are at their full length when the flower is open and the anthers have dehisced. The filaments are exserted in all species; they protrude from the throat of the corolla tube but do not necessarily surpass the lobes.

The style is filiform and always exserted, in some species surpassing the corolla lobes in pressed flowers. As is the case with the filaments, the style appears to elongate little after the flower is mature and the anthers have dehisced. In the majority of species the style always surpasses the filaments, the anthers never coming into direct contact with the stigma; in the species of sect. OMPHALOSTIGMA, the style is always overtopped by the filaments; in a few species of sect. LISIANTHIUS, the relative position of the two is variable.

The stigma is either capitate or peltate, and in contrast to most gentians, only indistinctly bilobed (FIGURE 5). The peltate type is more common in the genus, and it is probably the generalized type in that it resembles more closely the basic condition in the family. Most genera of Gentianaceae are characterized by having a deeply bilobed stigma with linear or lamellar lobes. The peltate type of stigma in *Lisianthius* resembles this generalized gentianaceous type, but the lobes are very small and somewhat connate on the adaxial surface. In addition the margins are reflexed, obscuring the apex of the style and causing the lobes to appear hemispherical. The capitate stigma is easily derived from the peltate type. In its extreme form, as found in *L. longifolius* and *L. cordifolius*, the stigmatic

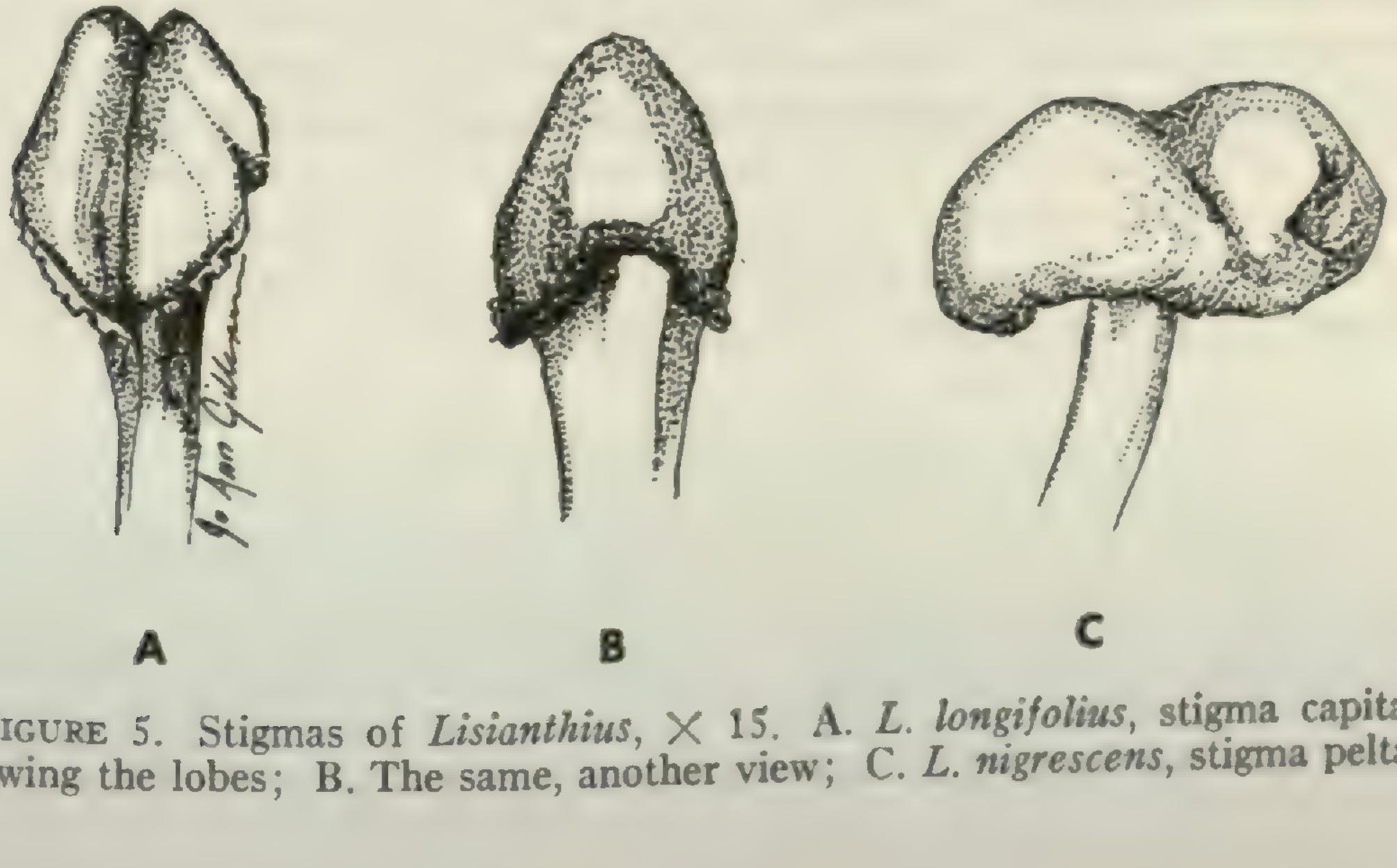


FIGURE 5. Stigmas of *Lisianthius*, × 15. A. *L. longifolius*, stigma capitate, showing the lobes; B. The same, another view; C. *L. nigrescens*, stigma peltate.

lobes are further reduced in size and are entirely connate along their adaxial surfaces; the margins are not at all reflexed. The stigmas of the closely interrelated *L. glandulosus*, *L. laxiflorus*, and *L. troyanus*, although capitate, are somewhat intermediate to the peltate type. In these species the lobes are small with barely reflexed margins, but they are not entirely connate.

Grisebach (1839) divided his genus *Leianthus* (= *Lisianthius*) into two sections based on their supposedly distinctive stigmatic types: sect. OMPHALOSTIGMA, with peltate stigmas, and sect. LISIANTHIUS, with capitate stigmas. Later (1845) Grisebach elevated sect. OMPHALOSTIGMA to generic rank, as *Petasostylis*, without changing its definition, and included within it *L. saponarioides* and *L. nigrescens*. At the same time he included in the genus *Leianthus* (his old section *Lisianthius*), *L. cordifolius*, *L. cuspidatus*, *L. exsertus*, *L. latifolius*, *L. longifolius*, and *L. umbellatus*. The genera were separated primarily by the type of stigma, as the sections were earlier. Actually, *L. nigrescens* and *L. saponarioides* are the species in which the form of the peltate stigma is most extreme. However, except for *L. longifolius* and *L. cordifolius*, all of the species included in *Leianthus* (*sensu* Grisebach, 1845), have definitely peltate stigmas.

Lisianthius nigrescens, according to my interpretation, is more closely related to all of the species included by Grisebach in *Leianthus* (*sensu* 1845) than it is to *L. saponarioides*. In fact it is so similar to *L. cuspidatus* that most authors have considered the two synonymous.

I have found the type of stigma to be nearly useless as a criterion in determining relationships in *Lisianthius*. The peltate and capitate types intergrade from species to species and sometimes, particularly in *L. auratus* and *L. seemannii*, within a species. Both types, in distinct form, are found in the Jamaican *L. longifolius*. *Petasostylis* has not been accepted by any authors since Grisebach, and there appears to be no reason whatever for maintaining it.

Fruits. The fruit is a semiwoody, bivalvate, loculicidal capsule. Upon dehiscence the placentae are visible as whitish, erose bands along the edge of the valves adjacent to the sutures.

The nearly mature capsule is generally flattened slightly on a plane perpendicular to the suture and is oblong-ellipsoid or fusiform in shape. However a few species in sect. LISIANTHIUS subsect. HERBACEI differ in that the capsules are ovoid in shape and not flattened. The two types are illustrated in FIGURE 6.

CHROMOSOME NUMBERS

The chromosome number of nine species was recently reported as $n = 18$ (Weaver, 1969). During the present study, the nine species listed below were investigated, and not a single deviation from the earlier reported number has been found:

L. adamsii (*Weaver 2342*)

L. auratus (*Weaver & Wilbur 2253*)
L. axillaris (*Weaver & Wilbur 2252*)
L. brevidentatus var. *brevidentatus* (*Weaver 2184*)
L. laxiflorus (*Weaver & Howard 2349*)
L. nigrescens var. *nigrescens* (*Weaver 2134*)
L. nigrescens var. *chiapensis* (*Weaver 2168*)
L. oreopolus (*Weaver 2173*)
L. peduncularis (*Weaver & Wilbur 2247*)
L. quichensis (*Weaver 2178*)
L. viscidiflorus (*Weaver 2179*)

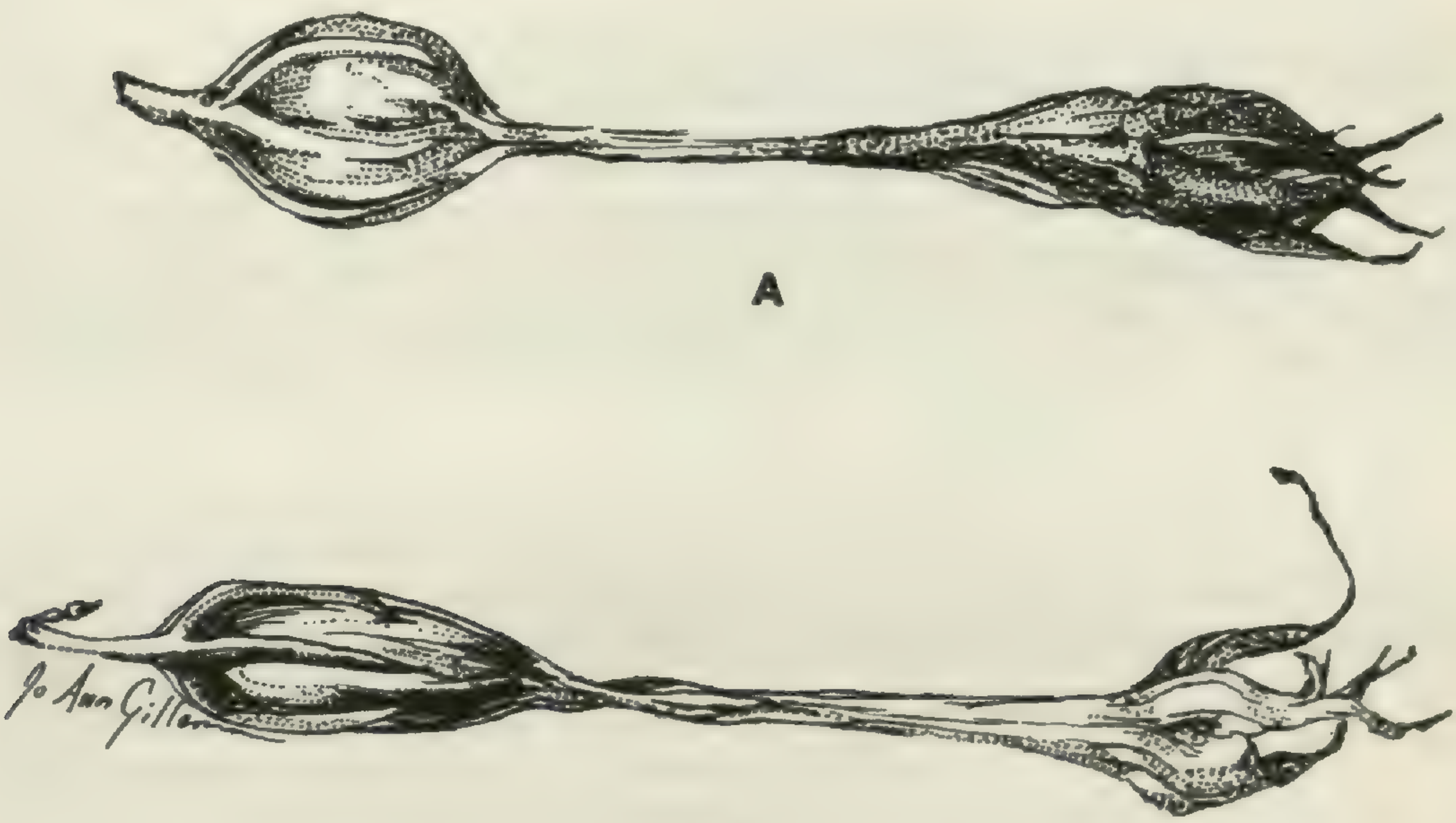


FIGURE 6. Capsules of *Lisianthius*, × 2. A. *L. nigrescens*, capsule broadly ovoid; B. *L. cordifolius*, capsule oblong-ellipsoid.

Flower buds were fixed in modified Carnoy's solution and the pollen mother cells were subsequently squashed in acetocarmine. Voucher specimens have been deposited at DUKE, except for *L. laxiflorus* which is at A.

With the exception of *Gentiana L.*, *Gentianella* Moench, and *Sabatia* Adans. little is known of the chromosome numbers in the Gentianaceae. However from a perusal of the summaries of chromosome numbers in the Gentianaceae (Rork, 1949, and Löve, 1953) and the chromosome indices, it appears that most of the larger genera are characterized by having more than one chromosome number. *Sabatia*, in which there is a wide array of numbers (Perry, 1967), is outstanding in this respect. *Halenia* Borkh., on the other hand is similar to *Lisianthius* in that all of the six species investigated, including representatives from both the Old and New World, are characterized by having the same chromosome number.

Although not all of the species have been investigated, a notable gap being the two species in sect. OMPHALOSTIGMA, change in chromosome number appears to have played no evolutionary role whatever within

Lisianthius. Nor has chromosome number been helpful in determining relationships within the genus. In the genera supposedly most closely related to *Lisianthius*, comprising the Gentianeae-Tachiinae of Gilg (1895), only two species, *Eustoma russellianum* G. Don, with $n = 36$ (Rork, 1949), and *Macrocarpaea thamnoides* (Griseb.) Gilg, with $n = 21$ (Weaver, 1969), have been investigated. Although these counts are too scanty to give more than a hint as to the relationships between *Lisianthius* and its supposed relatives, as previously pointed out by Weaver (*loc. cit.*), they do suggest a possible relationship between *Lisianthius* and *Eustoma*.

FLORAL ANATOMY

Various aspects of the floral anatomy of *Lisianthius* have been described by previous investigators. Perrot (1898) included three species, *L. exsertus*, *L. nigrescens*, and *L. longifolius* in his investigation of the anatomy of the Gentianaceae but limited his discussion of floral anatomy to the ovary of *L. nigrescens*. Woodson (1936) described the floral fibers of *L. brevidentatus*. Lindsey (1937, 1940) described in detail the vasculature of the flower of *L. longifolius*.

The anatomy of the flowers of 21 species was investigated during the course of the present study, with emphasis on the floral fibers and placentation. Flowers were infiltrated with paraffin using the tertiary butyl alcohol series suggested by Johansen (1940). The material was sectioned on a rotary microtome at 15 μ and stained in 1% Safranin in 95% EtOH and 1% Fast Green in 95% EtOH (Johansen, *loc. cit.*). Flowers of most of the species investigated were collected in the field and preserved in FAA. The flowers of the remaining species were taken from herbarium specimens and boiled in water immediately before infiltration.

The vascular traces to the calyx, corolla, and androecium of *Lisianthius* are variously supplied with heavily lignified elements. These elements were described by Woodson and illustrated (1936) from what he called *L. brevidentatus*. Woodson's material was collected by W. A. Schipp in British Honduras and was almost certainly *L. brevidentatus* var. *collinus*, since the typical variety of *L. brevidentatus* is not known from that country and *Schipp 1205* is the type and only collection of var. *collinus*.

According to Woodson (1936), these heavily lignified elements are primarily fibers of metaxylary origin with a few phloem or pericyclic fibers around the periphery of the bundles. They are most conspicuous in the calycine and corolline traces but are also found in the staminal traces when the stamens are still adnate to the corolla tube.

The present study has shown that there is considerable interspecific variation in the degree to which the fibers are developed, both in the same organ and among the various organs. Only in a very few species [*L. oreopolus*, *L. brevidentatus*, *L. viscidiflorus* (sect. LISIANTHIUS subsect. HERBACEI), *L. skinneri*, *L. longifolius*, *L. glandulosus* (sect. LISIANTHIUS subsect. FRUTICOSI), and *L. meianthus* (sect. OMPHALOSTIGMA)] are they well developed in the calyx, and then always more so in the tube

than in the lobes. In general, the fibers are poorly developed in the staminal traces. Only in *L. silenifolius*, *L. brevidentatus*, and *L. longifolius* are they at all conspicuous.

It is in the corolline traces that the fibers are most widespread in occurrence in the genus; they are well-developed in 15 of the 21 species investigated. In those species in which they occur, the fibers are poorly developed at the base of the corolla in fresh, newly opened flowers; however, in older flowers the fibers are well developed nearly to the base of the corolla. The development thus appears to be basipetal, as would be expected in a determinate organ. The fibers never extend into the corolla lobes.

The following species are well supplied with fibers in their corolline traces:

Sect. LISIANTHIUS

Subsect. HERBACEI	Subsect. FRUTICOSI	Sect. OMPHALOSTIGMA
L. brevidentatus	*L. adamsii*	*L. meianthus*
L. nigrescens	*L. auratus*	
L. oreopolus	*L. axillaris*	
L. quichensis	*L. cordifolius*	
L. silenifolius	*L. glandulosus*	
	L. laxiflorus	
	L. longifolius	
	L. skinneri	

In the following species the fibers are poorly or not at all developed in the corolline traces:

Sect. LISIANTHIUS

Subsect. HERBACEI	Subsect. FRUTICOSI
L. viscidiflorus	*L. capitatus*
	L. exsertus
	L. latifolius
	L. troyanus
	L. umbellatus

In all of the latter group of species, the marcescent corolla abscisses before the capsule matures and the seeds are shed. In the former group of species, except for *L. skinneri*, the corolla is more or less persistent on the mature capsule. Well developed fibers in the corolline traces obviously give support to the marcescent corolla and determine to a large extent the degree to which it persists.

Similar floral fibers were reported by Woodson (1936) to be present in *Coutoubea spicata* Aubl. (Helieae), *Canscora* Lam., *Centaurium* Gilib. (Gentianeae-Erythraeinae), and *Zygostigma* Griseb. (Gentianeae-Tachiinae) but not in those genera, e.g. *Chelonanthus* Gilg, *Macrocarpaea* Gilg, *Calolisianthus* Gilg, etc., of the Helieae and Gentianeae-Tachiinae included in *Lisianthius* by some authors.

According to Gilg, the Gentianeae-Tachiinae, of which *Lisianthius* is a member, are characterized by having unilocular ovaries. He illustrated

the ovaries of *L. nigrescens* (p. 92, *Fig. 41-J*) and *L. saponarioides* (p. 92, *Fig. 41-E*, actually *L. acuminatus* Perk., as will be explained later) as being unilocular. Perrot (1898) also described the ovary of *L. nigrescens* as being unilocular. However the present study has shown that all stages toward bilocularity, including complete bilocularity, are found in the ovaries of the various species.

The ovary of *Lisianthius* is bilocular at the base in all of the flowers examined. In most of the species, however, the septum becomes incomplete for 15 to 500 μ at the base of the placentae or below. As the placentae form, they abut and fuse and the ovaries appear bilocular again in the mid-portions. In five of the six species of sect. LISIANTHIUS subsect. HERBACEI (*L. brevidentatus* being the exception) examined, however, the placentae do not abut except in the upper portions, and the ovaries are unilocular for most of their length. Three of the species examined, *L. axillaris*, *L. skinneri*, and *L. latifolius*, in subsect. FRUTICOSI, are completely bilocular; *L. troyanus* and *L. laxiflorus* are bilocular except for a portion 15 μ in length where the septum is incomplete. In most of the species then, the ovaries are unilocular with parietal placentation but show varying tendencies toward bilocularity. A few species are bilocular with axile placentation.

Buds of *Lisianthius umbellatus*, a species characterized by having an almost completely bilocular ovary when mature, were sectioned at several stages in their development. In younger buds the septum is incomplete and the placentae completely separate. The arms of the septum and the inner surface of the placentae are covered with a distinct epidermis. In older buds the placentae abut as they enlarge; the epidermis then breaks down and the placentae fuse.

In those species where it is bilocular or nearly so, the ovary is flattened along an axis perpendicular to the septum, and the placentae are brought into close physical contact thus allowing fusion to take place. In the species of sect. LISIANTHIUS subsect. HERBACEI where it is unilocular for most of its length, the ovary is not flattened and the placentae are widely separated.

A few miscellaneous aspects of the floral anatomy of *Lisianthius* should be noted. Large crystals (druses) are found around the periphery of the basal portion of the ovary of *L. troyanus*. Crystals were not found in any other species of *Lisianthius*. Surrounding the basal portion of the ovary of all species investigated is a 5-lobed ring of densely staining, non-vascularized, glandular tissue. According to Lindsey (*loc. cit.*), ovaries glandular at the base are found in most of the genera associated with *Lisianthius* in the Gentianeae-Tachiinae by Gilg as well as those in the anatomically similar Helieae.

BREEDING SYSTEMS

The breeding systems of *Lisianthius* have not been studied in the field; the following observations were made from plants grown in the green-

houses of Duke University. All six species studied, *Lisianthius adamsii*, *L. capitatus*, *L. cordifolius*, *L. longifolius*, *L. nigrescens* (var. *chiapensis*) and *L. troyanus*, are self-compatible.

In all the species cited above, except *Lisianthius nigrescens*, the styles are considerably longer than the filaments, and the anthers do not come into physical contact with the stigmas. The flowers of these species are proterandrous and thus appear to be adapted for outcrossing. These plants, in fact, seldom set seed unless the flowers were artificially pollinated. In most populations of *L. nigrescens* var. *chiapensis*, on the other hand, at least some of the filaments in each flower are as long as the styles, and some of the anthers do come into direct contact with the stigmas. The flowers of members of this taxon are characterized by having the stigmas receptive as the anthers dehisce and thus are adapted for self-pollination. These plants invariably set seed profusely in the greenhouse without artificial pollination.

All species of *Lisianthius* have relatively showy flowers which produce copious amounts of nectar from glands at the base of the ovary, and although they are odorless, would seem to be quite attractive to animal pollinators. Little is known, however, of the pollinators of *Lisianthius*. No insects were observed on the plants in the field. Judging from the strikingly different colors of some of the flowers and the wide variation in flower form, particularly the shape and size of the corolla and the degree to which the styles and filaments are exserted, the various species are probably adapted to pollination by a wide variety of animals. In fact, specialization leading to pollination by different vectors has probably been a major evolutionary force within the genus.

Smaller bees of the genus *Bombus* were frequent visitors during the summer months to flowers of cultivated *Lisianthius adamsii*, *L. cordifolius*, *L. longifolius*, and *L. troyanus*. In all of these species the corolla tubes are relatively wide and the styles and filaments are well exserted. In addition the corolla lobes are widely spreading or even recurved, further exposing the anthers and stigmas. Bees invariably landed on the filaments and crawled into the corolla tube in search of the abundant nectar; they never came into contact with the anthers or the stigmas. Although *Bombus* is perhaps not a pollinator of the *Lisianthius* species in their native habitats, its behavior on cultivated plants strongly suggests that nectar-seeking bees are not effective pollinators of those species with well exposed anthers and stigmas.

These species are probably pollinated by various lepidopterans, pollen gathering bees, and/or hummingbirds. *Lisianthius saponarioides*, with erect flowers and short, narrow corolla tubes seems well suited to pollination by butterflies. Species in which the corolla tube is relatively broad and the anthers and stigmas held within the erect or slightly spreading corolla lobes are possibly pollinated by nectar-seeking bees. It appears that closely sympatric species of *Lisianthius* always differ strikingly in corolla and/or flower form.

POLLEN MORPHOLOGY

Nilsson (1970) has recently described the morphology of pollen grains of what he called "*Lisianthius s. lat.*" His study, based on acetolyzed grains observed both with the light microscope and scanning and transmission electron microscopes, included a large number of plants not referable to *Lisianthius* P. Browne. Only Nilsson's "*Longifolius*-type" is found in that genus; the following description is condensed from Nilsson's (*loc. cit.*, p. 4).

Pollen grains in monads, 3-colporate, subprolate to prolate, 28–50 × 23–40 μ. Colpi meridional, 2/3–3/4 of polar axis. Exine 3–5 μ thick. Sexine as thick as nexine, or thicker, reticulate or occasionally ± smooth. Lumina angular, ca. 0.5–7 μ in diameter. Muri ca. 0.5–1 μ wide.

According to Nilsson (1970), the plants here included in *Lisianthius* are homogeneous in their pollen type. Of the species examined, 21 are characterized by having grains with a finely reticulate sexine pattern; the coarseness of the reticulum varies intraspecifically as well as interspecifically and therefore appears to be of no taxonomic significance. Only *L. exsertus* varies significantly in its pollen morphology, and only in the sexine pattern which is nearly smooth when observed with the light microscope, but shows an intricate, very closely interwoven pattern in scanning pictures. The sexine of the grains of *L. exsertus* is basically the same as that in the other species, except that the lumina of the reticula are greatly reduced (Nilsson, *in litt.*)

According to Nilsson (1970) the pollen type found in *Lisianthius* (his *Longifolius*-type) is distinct from and not easily correlated with the pollen types of the other plants included in his study. (These plants and their relationship to *Lisianthius* has already been discussed.) It differs from the only other single-grain types in its prolate or subprolate grains with a fine reticulate pattern, relatively narrow muri, and more or less angular lumina, and in the absence of verrucoid processes (Nilsson, *loc. cit.*).

Nilsson (1970) found that *Lisyanthus loranthoides* Griseb., a Peruvian species, has pollen of his *Longifolius-type*. Grisebach (1839, 1845) placed this species in a monotypic section, CHORIOPHYLLUM, of *Lisyanthus* Aubl. (not the same as *Lisianthius* P. Browne), but suggested that perhaps it belonged in a separate genus. Macbride (1959), although not having seen any specimens of this taxon, suggested that *ex char.* it might be the same as *Macrocarpaea chlorantha* Gilg. An isotype of *L. loranthoides* (*Matthews 1315*, OXF) has been seen. With its conspicuously bifurcate stigmas, 4-angled stems, and calyx, with obtuse lobes, fused for nearly 2/3 its length, this species clearly is not referable to *Lisianthius* as here interpreted. Morphologically it appears to be somewhat intermediate between it and *Macrocarpaea*, and probably should, as Grisebach suggested, be placed in a distinct genus.

INTRAGENERIC RELATIONSHIPS

Chromosome number, floral anatomy, and pollen morphology have yielded few clues for determining relationships between the species of *Lisianthius*. Therefore a reliance on gross morphological features is necessary. Since there are few morphological trends within the genus, an infrageneric classification based on them must of necessity be highly subjective.

Lisianthius longifolius, the lectotype species of the genus, and the other species also characterized by basically tubular or funnelform corollas and unequal filaments inserted in the lower half of the corolla tube, form a logical group which I am calling section LISIANTHIUS. The remaining two species, *L. meianthus* and *L. saponarioides*, which differ strikingly by their salverform corollas and their equal filaments inserted near the apex of the corolla tube, seem to form a second group of equal rank to be called section OMPHALOSTIGMA.

Section LISIANTHIUS is comprised of two subsections, the HERBACEI with 7 species, monopodial, suffrutescent herbs with determinate main axes, usually compound dichasia, and sessile leaves, and the FRUTICOSI with 18 species, subshrubs, shrubs, or even small trees with indeterminate main axes, usually apparently simple dichasia, and petiolate leaves.

Section LISIANTHIUS subsect. FRUTICOSI is rather heterogeneous in a number of respects, and three subgroups are readily recognizable. Two Jamaican species, *Lisianthius umbellatus* and *L. capitatus* differ strikingly from all other members of the subsection in that their inflorescences appear capitate or umbellate owing to extreme reduction of all the branches. These two species comprise the series *Umbellati*. The remaining species are characterized by having diffuse inflorescences which are obviously dichasioid. However, one of these, the Jamaican *L. exsertus*,

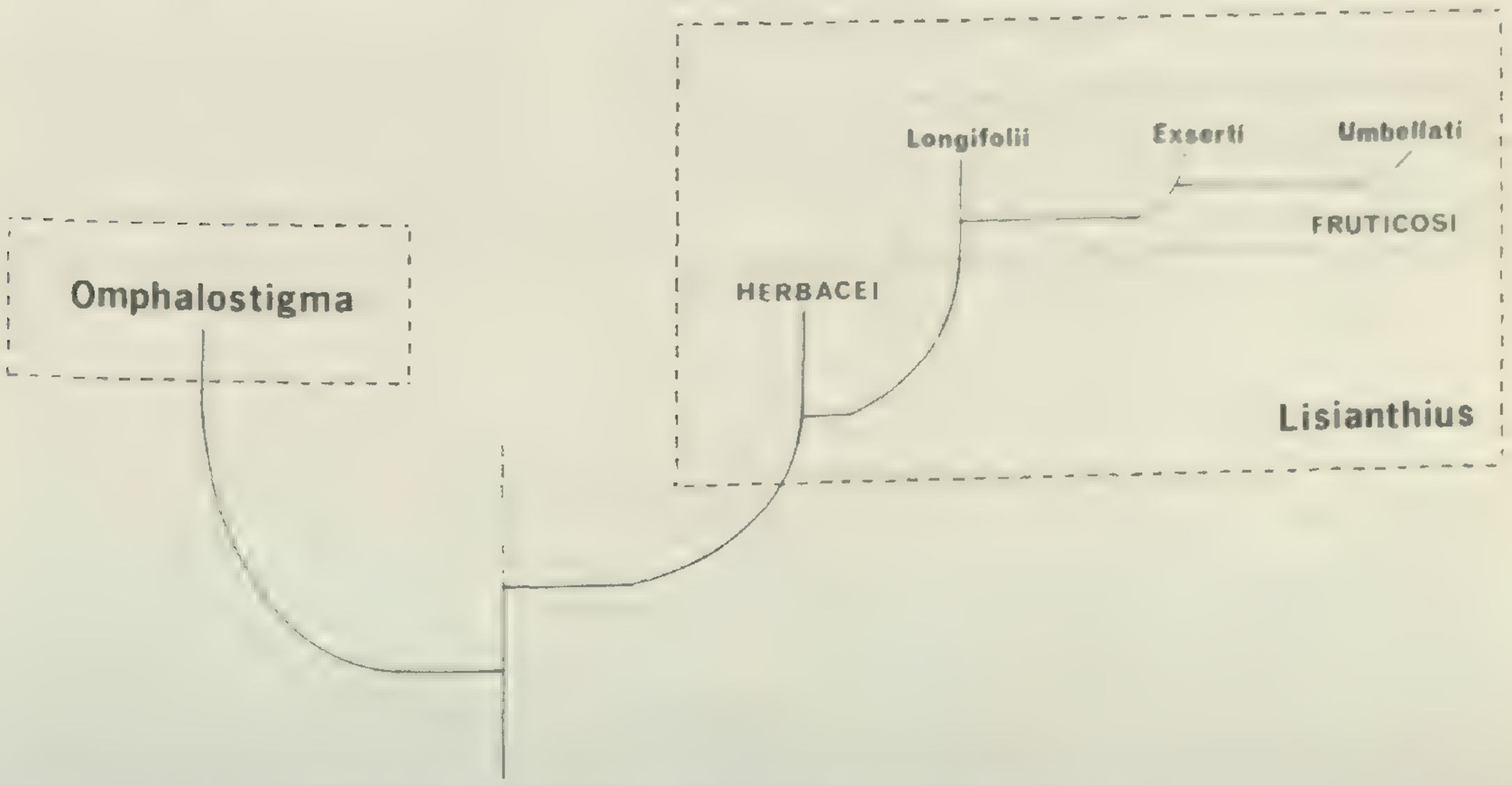


FIGURE 7. Probable relationships of the species groups in *Lisianthius*.

has flowers resembling *L. capitatus* in series *Umbellati* and is therefore intermediate between the species of that series and the remaining species in the subsection. In addition, the pollen of *L. exsertus* differs from that of all other members of the genus in having pollen with a nearly smooth rather than a distinctly reticulate sexine. On the basis of its somewhat intermediate position and its unique pollen, *L. exsertus* has been placed in a monotypic series, *Exserti*. The remaining fifteen species, still a rather heterogeneous assemblage, but all with diffuse inflorescences, tubular or funnelform corollas, and pollen with a reticulate sexine pattern, comprise the series *Longifolii*.

A suggestion as to the possible "phyletic" relationships between the various species groups is presented in FIGURE 7. This scheme is based almost entirely on gross morphological criteria and is highly conjectural. The generalized gentianaceous plant would appear to be somewhat as follows: a perennial, monopodial herb with a determinate main axis, inflorescences of compound dichasia, sessile leaves, rotate or salverform corollas, stamens of equal length in a given flower, and unilocular ovaries. If this type could be taken for the generalized one in *Lisianthius*, evolution has proceeded as follows: (1) from perennial herbs to annual herbs (rarely) in one direction and to subshrubs, shrubs or trees in the other; (2) from a determinate main axis to an indeterminate one; (3) from compound dichasia to apparently simple dichasia to solitary flowers; (4) from sessile leaves to distinctly petiolate ones; (5) from a salverform corolla to a tubular-funnelform one, with variations; (6) from stamens of equal length in a given flower to stamens of unequal length; and (7) from a unilocular to a bilocular ovary.

None of the extant species or species groups perfectly fits the hypothetical generalized type. The species in sect. OMPHALOSTIGMA approach it but differ in having petiolate leaves and nearly bilocular ovaries. Likewise, the plants of subsect. HERBACEI also approach the hypothetical prototype, but they differ in having tubular or funnelform corollas and filaments of unequal length. Therefore, both sect. OMPHALOSTIGMA and subsect. HERBACEI appear to be early offshoots from the primitive type. The plants of subsect. FRUTICOSI resemble those of subsect. HERBACEI in flower form, but differ in being fruticose, with indeterminate main axes, inflorescences of apparently simple dichasia, and petiolate leaves, all characters which deviate from the hypothetical prototype. Subsect. FRUTICOSI has very likely been derived from subsect. HERBACEI or from the line leading to it. The series *Exserti* and *Umbellati* are both offshoots from the main line in subsect. FRUTICOSI, leading to series *Longifolii*. The *Exserti* shares characters with both of the other series and presumably arose from the line leading to the *Umbellati*.

[*To be continued*]

THE MALPIGHIACEAE IN THE SOUTHEASTERN UNITED STATES[1]

KENNETH R. ROBERTSON

MALPIGHIACEAE A. L. de Jussieu, Gen. Pl. 252. 1789,
"Malpighiae," nom. cons.

(MALPIGHIA FAMILY)

Trees, shrubs [or frequently lianas], typically with unicellular medifixed trichomes. Leaves opposite [rarely alternate or whorled; two glands often present toward the base of the blades or on the petioles], simple and mainly entire. Inflorescences terminal [or axillary], usually a many-flowered, simple to compound raceme or cyme with jointed 2-bracteolate pedicels. Flowers perfect [rarely polygamous, sometimes dimorphic or cleistogamous with certain parts abortive], ± regular [to irregular]. Sepals 5, free or united below, generally quincuncially imbricate in aestivation, each with two glands on the abaxial surfaces [or glands solitary, absent, on some sepals only, or decurrent on the pedicels]. Petals 5, free, predominantly clawed, mainly cochlear imbricate. Androecium obdiplostemonous, the stamens 10 [5 or 15, rarely fewer by abortion, sometimes reduced to staminodia]; filaments often basally united. Gynoecium of 3 [2, 4, 5] united [to free] carpels; ovary superior, each locule with a single hemianatropous ovule pendulous from an axile placenta; styles as many as the carpels, free [or united]; stigmas terminal [or sublateral].

[1] Prepared for a generic flora of the southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of the National Science Foundation (Grant GB–6459X, principal investigator, Carroll E. Wood, Jr.). This treatment follows the format established in the first paper in the series (Jour. Arnold Arb. **39:** 296–346. 1958). The area covered includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants in this area, with additional information from extraterritorial taxa in brackets. References I have not seen are marked by an asterisk.

I extend my gratitude to Dr. Wood for his most helpful advice and editorial suggestions; to Dr. Bruce MacBryde (Pontificia Universidad Católica del Ecuador, Saint Louis University, and the Missouri Botanical Garden), whose thesis contains many frequently overlooked references, for reviewing the manuscript; and to Mrs. Nancy Dunkly for assistance with bibliographic problems and for typing the manuscript. A preliminary paper on the Malpighiaceae written by Charles James for the generic flora project has been consulted. Figures a–f of the illustration were drawn by the late Dorothy H. Marsh under the supervision of the late G. K. Brizicky from material collected by Joab L. Thomas; figures g–k are the work of Virginia Savage from material collected by George N. Avery.

Fruit a drupe [berry, nut, samara, schizocarp, or capsule]; seeds with little or no endosperm; embryo circinate [or prevailingly straight to curved.] TYPE GENUS: *Malpighia* L.

A family of 55–65 genera and 700–1300 species largely confined to the tropics and subtropics with the greatest diversification in tropical America. Only *Heteropteris* HBK. is represented in both hemispheres, with about 80 species in the Americas and *H. leona* (Cav.) Exell in West Africa. *Byrsonima lucida* (Miller) DC. is the only species of the family in our area, but *Malpighia glabra* L., *Janusia gracilis* Gray, *Aspicarpa hyssopifolia* Gray, *A. longipes* Gray, *A. humilis* (Bentham) A. Juss., and *Galphimia angustifolia* Bentham (*Thryallis angustifolia* (Bentham) Kuntze; [2] closely related to, or perhaps better included within, *G. brasiliensis* (L.) A. Juss.; cf. MacBryde) occur in the southwestern United States.

The Malpighiaceae are often divided into two subfamilies, Malpighioideae (Planitorae Niedz.) and Gaudichaudioideae A. Juss. (Pyramidotorae Niedz., Hiraeoideae Scholz in Melchior, nom. inval.), which are subdivided into six tribes based primarily on fruit morphology. Only tribe Malpighieae (fruits drupes or 1–3-locular nuts) is represented in our area. The Malpighioideae are neotropical shrubs or trees with flat floral receptacles and unwinged fruits, while the Gaudichaudioideae are pantropical, mostly lianas, usually with pyramidal receptacles and winged or crested fruits. MacBryde, however, has reported 3-angled pyramidal receptacles in *Verrucularia glaucophylla* A. Juss., of the Malpighioideae-Galphimieae, and has suggested that a reëvaluation of the traditional subfamilial division is needed.

The current system of classification is that of Niedenzu, which was based on the system proposed by A. Jussieu. As noted by C. V. Morton, "Although Niedenzu's taxonomic work is detailed and careful, he apparently made up his rules of nomenclature as he went along. . . . Perhaps more than any other taxonomist, Niedenzu found it necessary to subdivide groups, and so in the larger genera there are numerous subgenera, each with sections, subsections, and series and subseries. It is doubtful that this plethora of names is really necessary." Because of the methodology of Niedenzu, and that of various other authors, the nomenclature of much of the family is chaotic, although many problems have been clarified by the recent works of Morton, MacBryde, and Cuatrecasas.

Generally aligned with families included by Engler & Prantl in the Geraniales, the Malpighiaceae, Polygalaceae, Trigoniaceae, and Vochysiaceae were included by Scholz, Cronquist, and Thorne in their Rutales, Polygalales, and Geraniales, respectively. Others ally the Malpighiaceae with the Linaceae, Geraniaceae, Zygophyllaceae, Erythroxylaceae, and re-

[2] *Thryallis* Martius (1829; type species: *T. longifolia* Mart.) has been conserved over *Thryallis* Linnaeus (1762; type species: *T. brasiliensis* L.) for a small Brazilian genus. Thus, the name *Galphimia* Cav. (1799; type species: *G. glauca* Cav.) can be used without conservation for an American genus of about ten species, even though it is a taxonomic synonym of *Thryallis* L. (cf. Taxon **16**: 76, 77. 1967; **17**: 328. 1968).

lated families. Takhtajan places this latter group of five families in his Geraniales (derived from the Rutales, Saxifragales, and Dilleniales), while Hutchinson includes them in the Malpighiales (derived from the Tiliales, Bixales, and Dilleniales). Cronquist considers the origin of the Geraniales, Linales, and Polygalales to be from the Rosales via the Sapindales.

A distinctive feature of the family, although by no means confined to it, is the "Malpighian" type of trichome, which is unicellular, two-armed, and attached by a more or less medifixed stalk. Unbranched, stellate, glandular, and stinging trichomes also occur in the family. Complex, somewhat fleshy, paired glands visible to the naked eye frequently occur on the outside of the sepals and on the leaf margins, lower leaf surfaces, or petioles. The stomata are paracytic, and the wood is commonly diffuse-porous with a tendency for the simple-perforated vessels to be aggregated into radial chains or clusters. The parenchyma is prevailingly paratracheal, and the multiseriate rays are heterogeneous. Although the anatomy of many lianous species is normal, some have highly complicated stelar structures.

The known chromosome numbers (of about 30 species in 14 genera) suggest that considerable diversification through polyploidy and aneuploidy has occurred. Reported sporophytic chromosome numbers are 12, 18, 20, 22, 24, 34, 38, 40, 42, 54, 56, 58, 72, ca. 84. More than one chromosome number has been reported in *Byrsonima crassifolia*, *Galphimia angustifolia*, possibly *G. glauca*, *Hiptage Madablota*, *Malpighia glabra*, and *Stigmaphyllon ciliatum*.

Two basic pollen types are found in the Malpighiaceae. In the first the grains are 3(4, 5)-colporate, with the colpal furrows distinct, united at the poles (syncolporate) or bibranched (parasyncolporate), while grains of the second pollen type are 4- to ca. 24-porate, often with complex geometric shapes correlated with the number of apertures, and with vestigial furrows forming surface patterns. In her study of African and Madagascan genera (including four American genera for comparison), Lobreau found correlations between pollen morphology and certain androecial and gynoecial features and indications that Malpighiacean pollen is similar to that of the Hypericaceae and Caryocaraceae. Erdtman found palynological similarities with the Humiriaceae, Tremandraceae, Trigoniaceae, and Zygophyllaceae. A thorough study of New World genera is needed for confirmation of a correlation of pollen morphology and the established subfamilial classification.

Although actual pollination has been observed only in *Malpighia*, *Bunchosia* L. C. Rich. ex HBK., and *Hiptage* Gaertner, the flowers of most genera appear to be "bee flowers." There are striking similarities between the flowers of certain Malpighiaceae and those of some species of *Oncidium* (Orchidaceae), but little has been published about this remarkable convergence. The floral mechanism of *Hiptage Madablota* is said to resemble that of *Aesculus* (Hippocastanaceae). Dimorphic to highly modified cleistogamous flowers occur in certain genera.

The embryo sac is usually tetrasporic, 16-nucleate and of the Penaea type. *Galphimia glauca* and *G. gracilis* have bisporic, eight-nucleate, Allium-type embryo sacs. Species of *Heteropteris* HBK., *Stigmaphyllon* A. Juss., *Banisteria*, *Hiptage*, and *Aspicarpa* L. C. Rich. that have been investigated show nucellar polyembryony with fertilization evidently not occurring. (Fertilization has been reported only in *Malpighia glabra*, but it probably occurs in *Tristellateia australis*.) Further studies are needed to ascertain the extent and effects of apomixis in the family.

Fossil materials, mostly leaves and fruits, allegedly representing Malpighiaceae have been reported from the Middle Cretaceous to the Pliocene. Unlike members of numerous other families that are primarily tropical today, the Malpighiaceae evidently did not occur in the paleoflora of the present-day Arctic Zone, although the family is recorded from the Tertiary flora of Europe.

The economic uses of members of the Malpighiaceae are few, considering the family's size. Extracts and infusions from certain species are used as narcotics, folk medicines, insecticides, pigments, and tanning agents. Certain South American Indian tribes, primarily in the Amazon and Orinoco river basins, prepare hallucinogenic infusions variously known as *caapi*, *ayahuasca*, *yajé*, *natema*, and *pinde* from species of *Banisteriopsis* C. B. Robinson ex Small. The most commonly used species is *B. Caapi* (Spruce ex Griseb.) C. V. Morton, which contains the β-carboline alkaloid bases harmine, harmaline, and *d*-tetrahydroharmine. Harmine has also been isolated from *B. inebrians* C. V. Morton and from *Cabi paraensis* Ducke, a species used as a folk medicine but evidently not as a hallucinogen. Such harmala alkaloids do not occur in *B. Rusbyana* (Niedz.) C. V. Morton, a species used as an additive in hallucinogenic beverages, but relatively high concentrations of N, N-dimethyltryptamine and traces of other tryptamines do occur. A narcotic drink is also made from *Tetrapteris methystica* R. E. Schultes, on which chemical studies have not yet been made. It seems likely that other genera and species of Malpighiaceae will be found to be used as narcotics, medicines, and poisons by aboriginal peoples.

The fruits of *Byrsonima*, *Bunchosia*, and *Malpighia* species are edible, and the drupes of *Malpighia glabra* L.,[3] Barbados or West Indian Cherry, Acerola, Cereza, contain exceptionally high amounts of Vitamin C, from 15 to 100 times the concentration found in oranges. This species is grown to some extent in Florida, Hawaii, and the West Indies, and vitamin tablets and frozen or canned juice made from the fruits are commercially available. The fibrous stems of *Heteropteris umbellata* and *Banisteria longifolia* are used for roping and basketry binding respectively. Strong and attractive wood used in furniture and construction is obtained from the arborescent species of *Byrsonima*. Many species are quite ornamental

[3] *Malpighia glabra* L. and *M. punicifolia* L. have been considered to be either conspecific or distinct, with the cultivated plants placed in either species or thought to be hybrids between them.

and are in cultivation in the tropics and in conservatories, although not to the extent that they deserve. Species of *Bunchosia*, *Byrsonima*, *Galphimia*, *Heteropteris*, *Malpighia*, and *Stigmaphyllon* are cultivated to some extent in Florida and southern California.

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Subfamily MALPIGHIOIDEAE

Tribe Malpighieae

1. **Byrsonima** L. C. Richard ex Humboldt, Bonpland & Kunth, Nov. Gen. Sp. **5**: ed. fol. 113, ed. qu. 147. 1822.[4]

Low spreading shrubs to small [or large] trees [rarely lianas], often much branched; bark warty [or smooth]; glabrescent, with the simple or T-shaped, often rust-colored trichomes largely confined to the younger parts [or the leaves, peduncles, pedicels and twigs densely pubescent]. Leaves opposite, glandless, simple, entire, usually coriaceous, sessile or shortly petiolate; petioles mostly stout; blades obovate-spatulate [or ovate to circular], the upper surfaces commonly glossy when alive but becoming glaucous upon drying; stipules axillary [or interpetiolar] and mostly connate, small and persistent. Flowers pedicellate, the pedicels jointed and 2-bracteolate, in terminal, many-flowered, simple racemes (occasionally compound at the base). Sepals 5, persistent, in anthesis the distal portion incurving between the petal claws and forming a constriction around the ovary and base of styles, the tips recurving; abaxial glands 2 on each sepal, contiguous, somewhat fleshy [or absent]. Petals 5, glabrous, subequal [to distinctly unequal], white to pink or red [or yellow], turning a deeper color with age; claws long, recurved; blades strongly concave, reniform to subcircular with undulate and ± entire [to slightly toothed] apices. Stamens 10, nearly equal in length, all bearing anthers; filaments thick, flattened and connate below, pubescent inside; anthers basifixed, 2-locular and introrse at anthesis, glabrous [or pubescent], connectives thick [and often forming prominent apical appendages]. Gynoecium syncarpous, 3-carpellate; ovary 3-lobed, conical [ovoid or globose], glabrous; styles 3, free, terminal, glabrous, slender, ± straight, tipped by the subulate stigmatic surfaces; receptacle flat or slightly concave, densely pubescent. Fruit a green, yellow, orange, red or brown globose [ovoid or conical] drupe, crowned by the persistent styles; stone solitary; pericarp rather thick and fleshy; endocarp hard, woody, pitted [or smooth], angular, 3-seeded, rarely fewer seeded by abortion. Seeds subglobose; embryo circinate, the cotyledons subequal, terete. Lectotype species: *Malpighia spicata* Cav. = *Byrsonima spicata* (Cav.) DC.; see J. K. Small, N. Am. Fl. **25**: 166. 1910.[5] (Name from Greek, *byrsa*,

[4] The generic name is usually attributed to L. C. Richard ex A. L. de Jussieu (1811). However, De Jussieu merely suggests that it might be possible to follow Richard's idea of separating *Malpighia* L. into three genera, *Malpighia, Byrsonima,* and *Bunchosia*; he does not indicate that he adopts this division. Also see discussion in MacBryde.

[5] Humboldt, Bonpland & Kunth referred *M. spicata* Cav. and seven other species of *Malpighia* to *Byrsonima* but did not make the formal transfers. It remains for a

FIGURE 1. **Byrsonima.** a–k, *B. lucida*: a, flowering branch, × 1; b, flower, × 5; c, calyx, showing glands on one sepal (glands on adjacent sepals removed), × 7; d, vertical section of flower — ovule and placentation shown semidiagrammatically, × 5; e, oblique side-view of stamen with anther sacs (to right) protruding below enlarged connective (to left), × 14; f, adaxial surface of stamen showing four anther sacs, × 14; g, fruit, × 2; h, pitted stone of fruit, × 4; i, diagrammatic cross section of stone (hatched) showing an embryo in section in each locule, × 4; j, k, opposite sides of the same embryo to show position of cotyledons, oriented as in seed, × 6.

hide, and Latin *nimia*, very much (used), in reference to the use of the bark in tanning leather.)

A tropical American genus of more than 100 species ranging from southern Florida, the West Indies, and Mexico to Bolivia and southern

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monographer to determine whether this species chosen by Small can be considered to be part of the protologue and thus eligible to be the lectotype or whether one of the ten species described under *Byrsonima* would be a more appropriate choice.

Brazil. Many species grow in dry or harsh habitats such as savannas, rocky hills, coastal thickets, serpentine and palm barrens, and pinelands; other species occur in selvas (tropical rain forests) and montane or cloud forests. *Byrsonima*, *Alcoceratothrix* Niedz. (usually included in *Byrsonima*), *Diacidia* Griseb., *Burdachia* A. Juss., and *Glandonia* Griseb. constitute subtribe Byrsoniminae Niedz.

The genus is represented in our area by *Byrsonima lucida* (Miller) DC. (including *B. cuneata* (Turcz.) P. Wilson; cf. Sargent, 1921), locustberry, a plastic species varying in habit from low spreading shrubs less than a meter high to trees exceeding eight meters with trunks 25 cm. in diameter. Distinguished by small spatulate-obovate leaves, elongate inflorescences with small bracts, pinkish flowers, glabrous anthers, pubescent filaments, and connectives much shorter than the anther sacs, *B. lucida* occurs in pinelands, low woods, and hammocks in the Everglades and Florida Keys and throughout most of the West Indies from the Bahamas to Barbuda and Trinidad.

Following his penchant for subdividing taxa, Niedenzu (1928) divided *Byrsonima* into two subgenera, four sections, eight subsections, twelve series, and four subseries. In his system, *B. lucida*, along with three West Indian and six South American species, was placed in subgen. BRACHYZEUGMA, sect. SERICOLEPIS, subsect. *Psilotheca*, series *Dictyoneura*, subseries *Glossolepis*. The correct sectional name is EPIPHYLLARION Griseb.; C. V. Morton (1968) chose *B. lucida* as the lectotype of this section.

The genus needs a thoroughly documented modern taxonomic revision conducted on a broad geographic basis to delimit and classify the species and subgeneric taxa accurately and to apply the current rules of nomenclature uniformly.

Only *Byrsonima verbascifolia* (L.) DC. has been studied palynologically. The grains are 3-colporate with lalongate ora, prolate, rounded-triangular to subcircular in polar view, and with a reticulate exine. Similar pollen is found in tribe Galphimieae Niedz. Other genera of tribe Malpighieae which have thus far been examined (*Malpighia* and *Bunchosia*) have porate pollen.

Although quite ornamental, *Byrsonima lucida* is infrequently cultivated. *Byrsonima crassifolia* (L.) HBK., $2n = 20, 24$ (including *B. cotinifolia* HBK.; leaves large, elliptic or rarely somewhat obovate, flowers yellow to reddish), *B. coccolobifolia* HBK. (leaves large, subcircular to broadly ovate or obovate, flowers pink to red, connectives much longer than the anther sacs), and *B. spicata* (Cav.) DC. (leaves large, elliptic with acute apices, flowers yellow) are also grown to a limited extent in Florida.

The fruits of all *Byrsonima* species reputedly are edible, and some are sold in local markets in Latin America. The wood of arborescent species is strong and heavy, has a reddish color, and is used for furniture and construction or is converted into charcoal. Certain species are used in tanning leather, as a source of inks, dyes or paints, and in folk medicine as an astringent and for the treatment of wounds, fevers, colds, diarrhea, snake bites, and leg tumors!

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MORPHOLOGICAL STUDIES IN CORDYLINE (AGAVACEAE) II. VEGETATIVE MORPHOLOGY OF CORDYLINE TERMINALIS

J. B. Fisher and P. B. Tomlinson

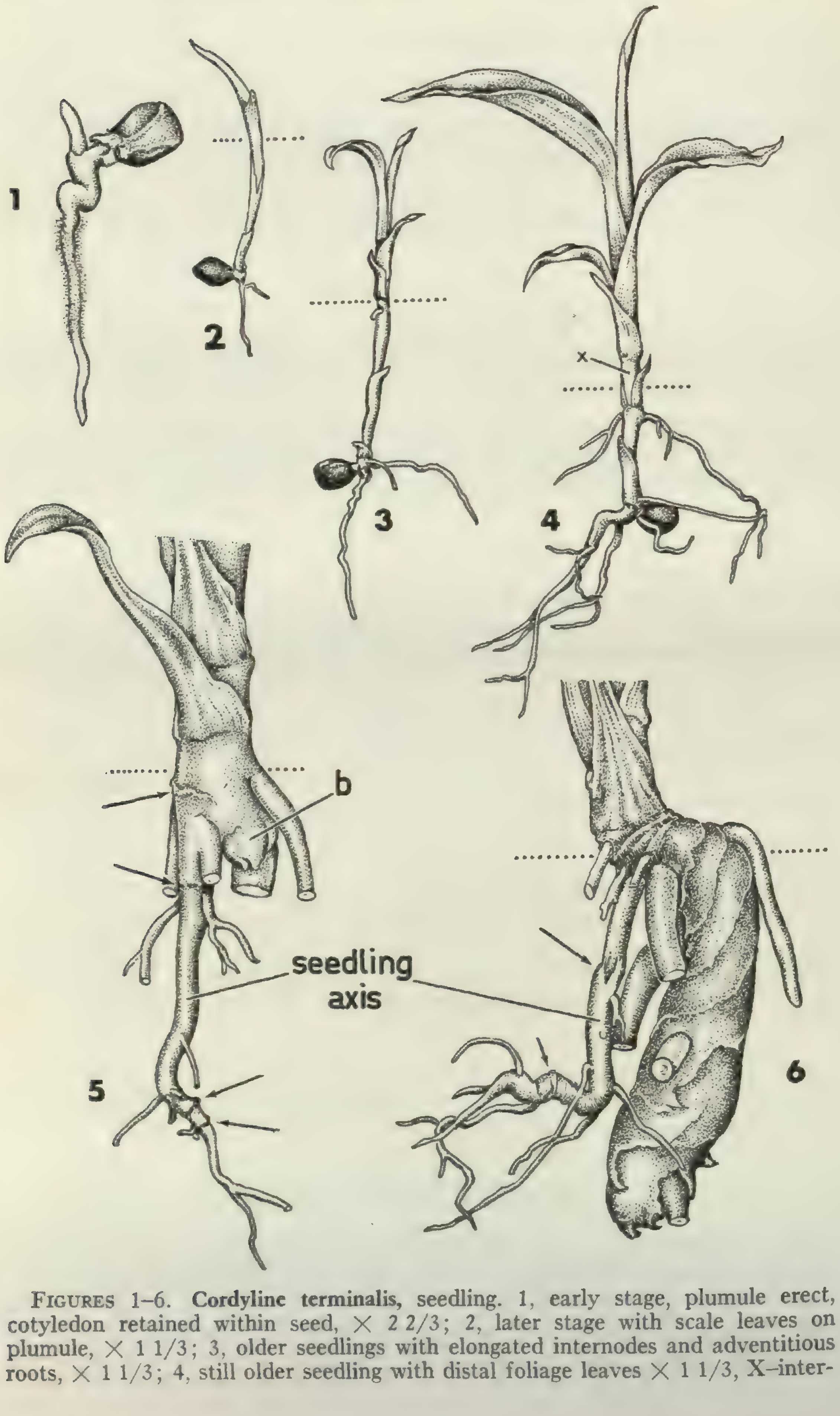
In an introductory paper in this series we described in a general way the growth habit of many species of *Cordyline* and the way it is related to a distinctive seedling morphology (Tomlinson & Fisher, 1971). We now restrict our inquiry to *C. terminalis*, the most widely cultivated species, describing its vegetative morphology in detail. This is the first comprehensive study of branching pattern in any member of the Agavaceae (*sensu* Hutchinson, 1959), and serves as a basis for future experimental work on the controlling factors of apical dominance, rhizome initiation, and secondary growth in this species. The continuing work will be reported in future articles. *Cordyline terminalis* grows rapidly and is easily propagated clonally so that it is an ideal experimental subject. It is therefore more suitable for experimental analysis than *Dracaena fragrans*, which was used initially as a subject for a reappraisal of the structure and growth of monocotyledons with secondary thickening (Tomlinson & Zimmermann, 1969; Zimmermann & Tomlinson, 1969; 1970).

Cordyline terminalis is probably native to the western Pacific and was at one time widely used as a food plant throughout Oceania (Barrau, 1961). The starchy underground rhizomes, erroneously called "root tubers," were cooked before being eaten. The leaves were used to wrap food, as a source of fiber, and even as clothing (largely ornamental). These uses have been supplanted by other food crops, but *C. terminalis* is still a widely cultivated ornamental. It forms, for example, the chief constituent of the living fences around the "gardens" of villagers in the highlands of New Guinea. There are numerous varieties referred to in horticultural literature (e.g., Graf, 1963). These differ chiefly in the color, shape, and size of the foliage leaves.

The usefulness of the shoot system of this species for experimental morphology was appreciated by Sachs (1882) and Goebel (1905) but their studies were preliminary and inconclusive. The underground rhizomes were described briefly by Troll (1937; p. 722).

MATERIAL AND METHODS

Most observations were made on large, field-grown plants up to 20 feet tall growing at Shaw's Nursery, 57th Ave., South Miami, Florida. These specimens included several varieties of unknown origin. Seeds were collected from mature fruits and sown in pots in a greenhouse to provide plants in early stages of development.



FIGURES 1–6. **Cordyline terminalis,** seedling. 1, early stage, plumule erect, cotyledon retained within seed, × 2 2/3; 2, later stage with scale leaves on plumule, × 1 1/3; 3, older seedlings with elongated internodes and adventitious roots, × 1 1/3; 4, still older seedling with distal foliage leaves × 1 1/3, X–inter-

For general anatomical observation, free-hand sections of fresh or FAA-fixed material were stained with aqueous solutions of either toluidine blue or basic fuchsin.

SEEDLING DEVELOPMENT

Germination in *Cordyline terminalis* is hypogeous (FIGURE 1), the greater part of the cotyledon remaining within the seed, and both cotyledon and seed remaining below soil level. This contrasts with the epigeous germination of *C. australis* and *C. banksii* which we have described and illustrated elsewhere (Tomlinson & Fisher, 1971; *Figs. 1, 2*). In these species only the tip of the cotyledon remains within the seed, the whole organ elongating and becoming erect; usually bringing the seed with it. Despite these early differences, late stages of seedling growth seem very similar in all species of *Cordyline*. The early differences are much more pronounced than those which Arnott (1962; p. 47) described in *Yucca* when he distinguished "hypogeous" from "epigeous" species. In both his types, the cotyledon does rise above the soil surface, although its tip is still within the seed coat, which may or may not remain buried. Later stages of *C. terminalis* are illustrated in FIGURES 2–6. The first plumular leaves are scale-like and there is a gradual transition to progressively larger foliage leaves. This should be contrasted with *C. australis*, where plumular leaves, though reduced, are green and never scale-like (cf. Tomlinson & Fisher, 1971; *Figs. 1–4*). The lowest, often underground, internodes are sometimes elongated (FIGURES 2–4), as in *C. australis*. Adventitious roots are developed on all parts of the seedling axis, but predominantly at the nodes. Successive internodes are progressively wider (FIGURE 5) in the manner normal for establishment growth in monocotyledons (Tomlinson & Zimmermann, 1966).

A major departure from normal monocotyledonous seedling development is then seen with the production of a descending (positively geotropic) rhizome from a bud in the axil of one of the lowest leaves (FIGURE 5, b). This repeats the peculiar pattern of seedling growth we described for other *Cordyline* species, in which the original seedling axis, displaced by this lateral rhizome, persists only as a pseudolateral appendage on older seedlings (FIGURE 6).

POST-SEEDLING DEVELOPMENT

The sapling subsequently develops as an apparently single axis which consists of the ascending, foliage-bearing aërial shoot continuous below

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node in which secondary vascular cambium first develops; 5, base of mature seedling, rhizome bud at b; 6, later stage with seedling rhizome well developed × 2 2/3, the original seedling axis as an apparent appendage. Arrows indicate nodes on original seedling axis. Larger roots cut off in FIGURES 5 and 6. A diagram representing FIGURE 6 is given in FIGURE 7 A.

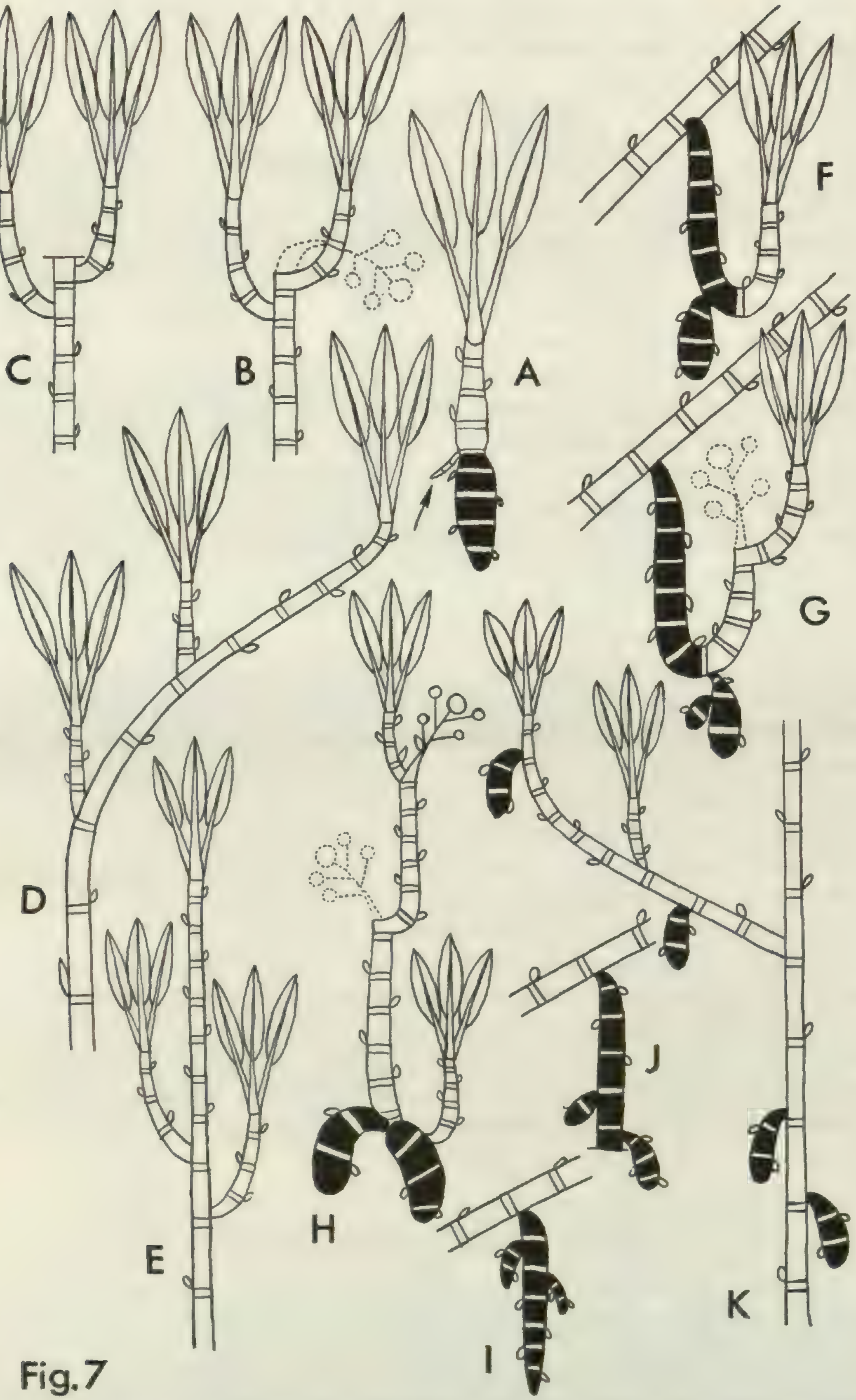
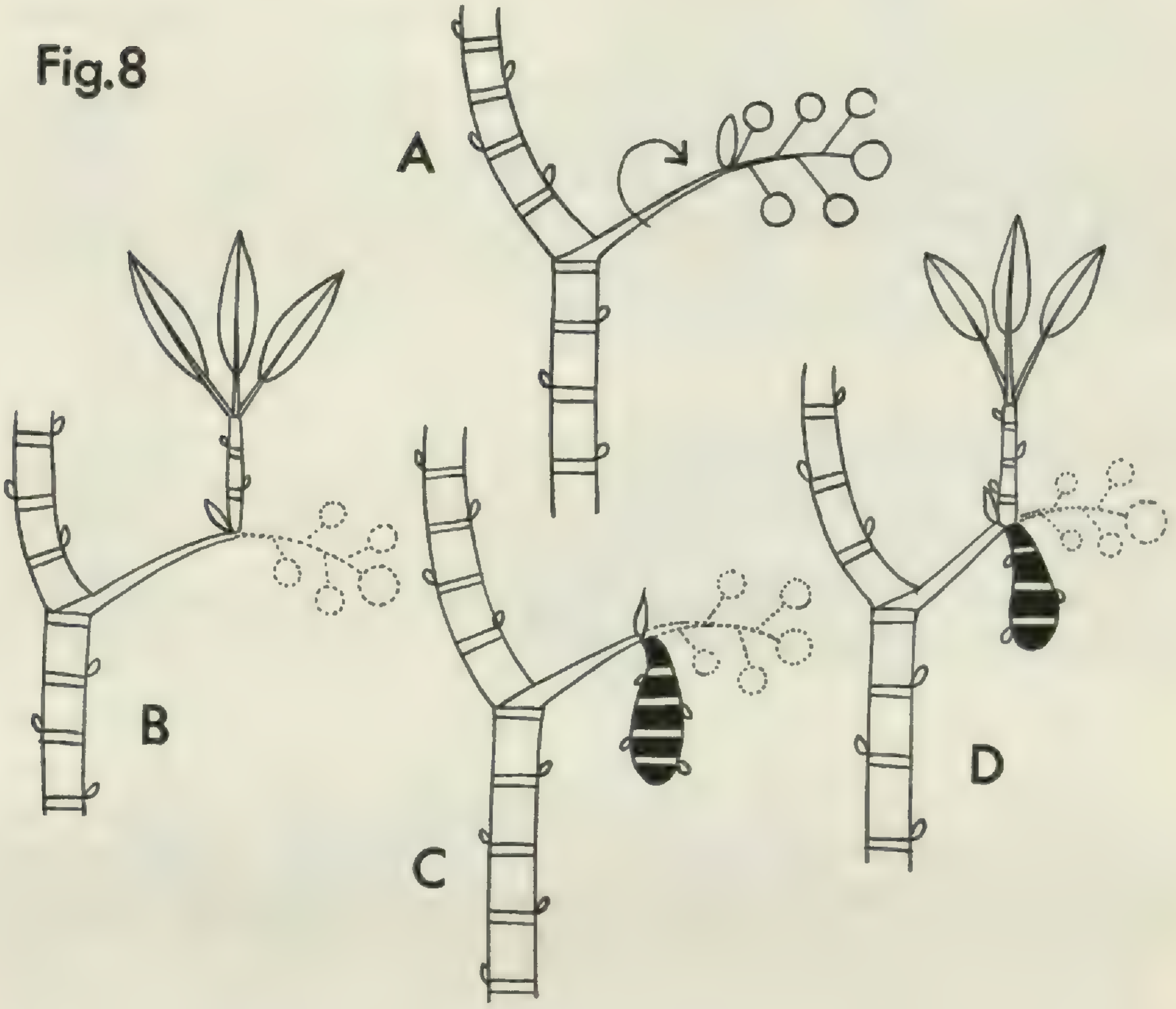


Fig. 7

FIGURES 7 and 8. **Cordyline terminalis,** shoot morphology represented diagrammatically. Leafy shoots are represented in outline with each node (double line) bearing a bud. Rhizomes shown solid black with each node (white line) bearing



a bud. Inflorescence represented by branched structures with circles; sites of former inflorescences are represented by dotted outline.

FIGURES 7 A–K. Branching on vegetative parts. A, sapling axis with original seedling axis displaced (arrow); B, forking of sympodium by production of two axillary branches below a terminal inflorescence; C, forking of stem by production of two axillary branches below injured or decapitated apex; D, leafy shoots from upper side of a leaning stem; E, leafy shoot from basal buds of an erect stem; F, aërial rhizome turning erect as a leafy shoot, the original rhizome producing a branch rhizome; G, leafy reversion shoot, flowering; branch rhizome itself branched; H, leafy shoot arising directly from rhizome at base of an erect sympodium; I, rhizome on lower side of leaning branch, branching *proximally* behind intact apex; J, rhizome on lower side of a leaning branch, branching *distally* behind injured or decapitated apex; K, typical position of aërial rhizomes on leafy shoots, on lower surface of a leaning branch, and at base of an erect shoot. Specimens which illustrate some of these diagrams are: A = FIGURE 6; B = FIGURE 14; C = FIGURE 9; F = FIGURES 18–20 (various ages).

FIGURES 8A–D. Vegetative proliferation at base of inflorescence. A, terminal inflorescence evicted by an axillary branch, the lowest bract subtending a flower-bearing branch (the twist of the base of the inflorescence is shown by the arrow); B, the same, with the lowest flowering branch replaced by a leafy shoot; C, the same, with the lowest flowering branch replaced by an aërial rhizome; D, the same, with the lowest flowering branch replaced by a leafy shoot plus a rhizome. Specimens which illustrate these diagrams are: A = FIGURE 11; B = FIGURES 21, 22; C = FIGURE 23.

with the descending scale-bearing rhizome. This is represented diagrammatically in FIGURE 7 A, with the displaced seedling axis shown as an apparently lateral appendage (arrow). Shoot construction in the adult plant eventually becomes seemingly diverse. However, this diversity is based on a few very simple rules of branching. The various ways in which these rules can be expressed are illustrated diagrammatically in FIGURES 7 and 8. These are all based on observed examples some of which are shown in FIGURES 9–26. The examples which correspond to a particular diagram are cross-referenced in the legends to these illustrations.

The morphological rules which govern this apparent elaborateness are simple. All leaves subtend a single bud. Buds are normally strongly inhibited and remain inconspicuous (e.g., FIGURE 14; b. They are not drawn to scale in FIGURES 7 and 8). Buds may grow out as either leafy shoots or as scale-bearing rhizomes. Rhizomes may become transformed directly into leafy shoots, but never vice-versa.

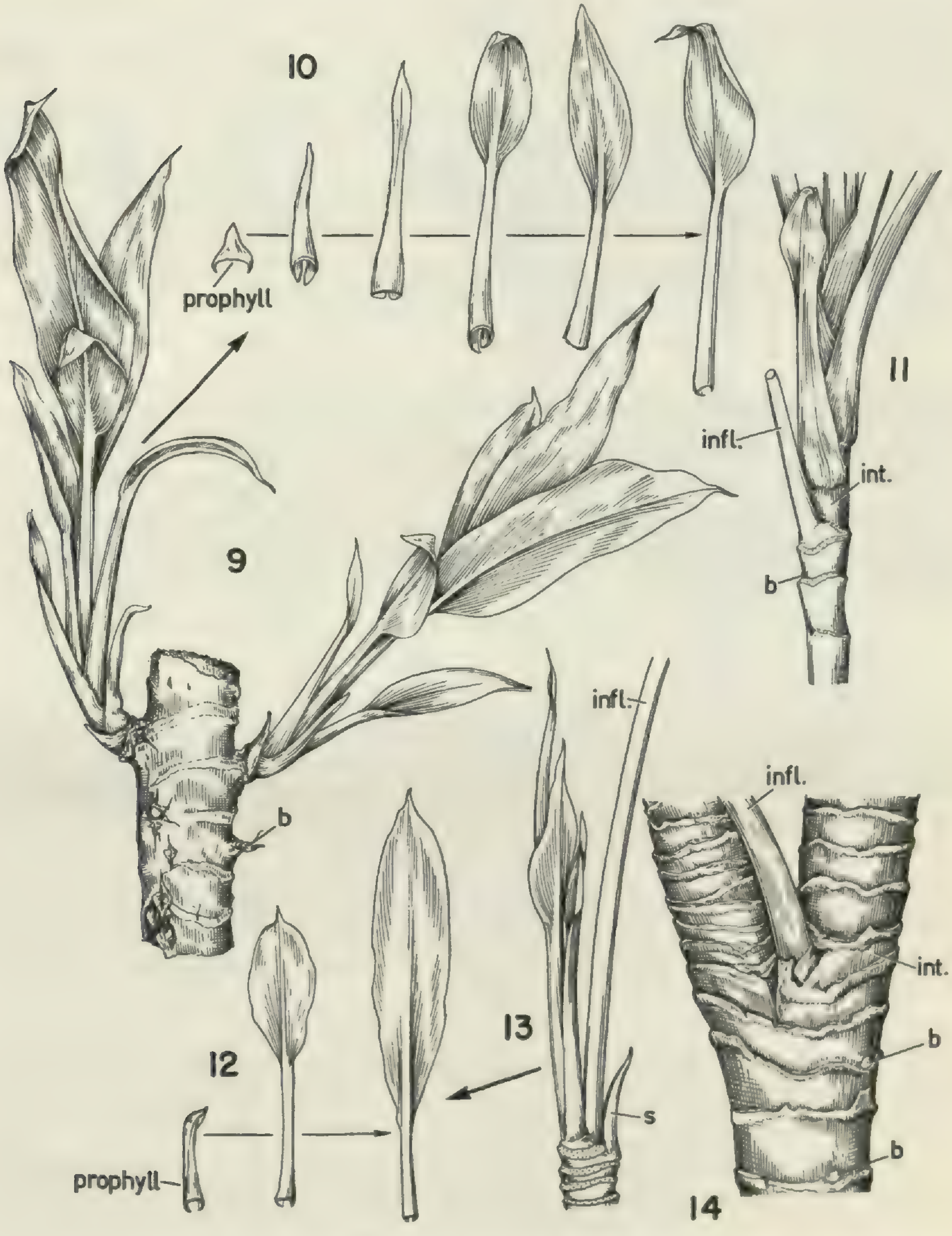
Three main categories of branch expression can be recognized, and these are described separately.

Leafy shoots. The commonest type of branching in undisturbed shoots involves normal sympodial development by substitution of a terminal inflorescence (FIGURE 7 H). Usually the bud in the axil of the foliage leaf immediately preceding the first bract of the inflorescence (i.e. at the base of the long peduncle (FIGURE 13), grows out as the substitution shoot. The first internode of this branch elongates (FIGURE 11, int.) to about the same extent as internodes on the parent axis so that there is no major articulation in the axis of the sympodium at the level of branching. Where buds from two successive nodes grow out, the sympodium itself branches and the axis is forked (FIGURES 7 B; 14). In this type of substitution growth, in which there is little delay in the development of the bud, its prophyll usually has a distinct lamina (FIGURE 12, prophyll) and the transition to foliage leaves along the branch is abrupt. Thus the second or third leaf of the continuing shoot has a more or less normal shape and size (FIGURE 12).

Essentially the same development occurs in the outgrowth of one or more buds below a damaged or decapitated apex as shown in FIGURES 7 C and 9. However, in these examples the bud has previously been subjected to a long period of inhibition. This is reflected in the outgrown shoot which has a short, scale-like prophyll without any indication of a lamina (FIGURE 10, prophyll) together with a longer series of transitional leaves before the normal foliage leaves are developed (FIGURE 10). Another difference is that the first few internodes do not elongate and there is consequently a more pronounced articulation at the insertion of the branch.[1]

Axillary buds on the upper side of leaning branches may grow out as leafy shoots (FIGURE 7 D). Buds at the base of tall erect stems may also

[1] These differences between early ("precocious") and late-developing branches correspond to those seen in woody dicotyledons, where they have been distinguished as "sylleptic" and "proleptic" shoots (Tomlinson & Gill, unpublished).



FIGURES 9–14. **Cordyline terminalis,** outgrowth of buds as leafy shoots. 9, two renewal branches below a decapitated apex, × 1/2; 10, six successive leaves from base of one of the branches shown in FIGURE 9, × 1/2, prophyll (first leaf) to left; 11, renewal shoot below terminal inflorescence only base of which (infl.) is shown, × 1/2, int. = first internode on renewal shoot; 12, three successive leaves from base of the branch shown in FIGURE 11, × 1/6, prophyll (first leaf) to left; 13, development of shoots from two buds below a terminal inflorescence, × 1/2, the right-hand (lower) shoot (S) at a much earlier stage than the left-hand (upper) shoot; 14, forking sympodium × 1, produced by equal development of two buds below a terminal inflorescence (infl.); int. = lowest internode of right-hand branch; b = inhibited buds. Diagrams which correspond to these illustrations are: 9 = FIGURE 7 C; 14 = FIGURE 7 B.

grow out in the manner of epicormic shoots (FIGURE 7 E), presumably because they are distantly removed from an inhibiting source. This tendency to branch by basal suckers is responsible for the "shrubby" habit of *Cordyline terminalis* in contrast to the tree habit of other species, as we described in our introductory paper.

All these methods of shoot development are precisely as reported for other arborescent Agavaceae (Tomlinson & Zimmermann, 1969).

Rhizomatous shoots. *Cordyline terminalis* does differ from almost all other Agavaceae because the rhizomatous shoot which is characteristic of the seedling also occurs on aërial branches. For convenience we refer to these as "aërial rhizomes," although we appreciate that there may be semantic difficulty in referring to above-ground shoots as rhizomes. Similar aërial rhizomes are developed in *Cordyline stricta*.

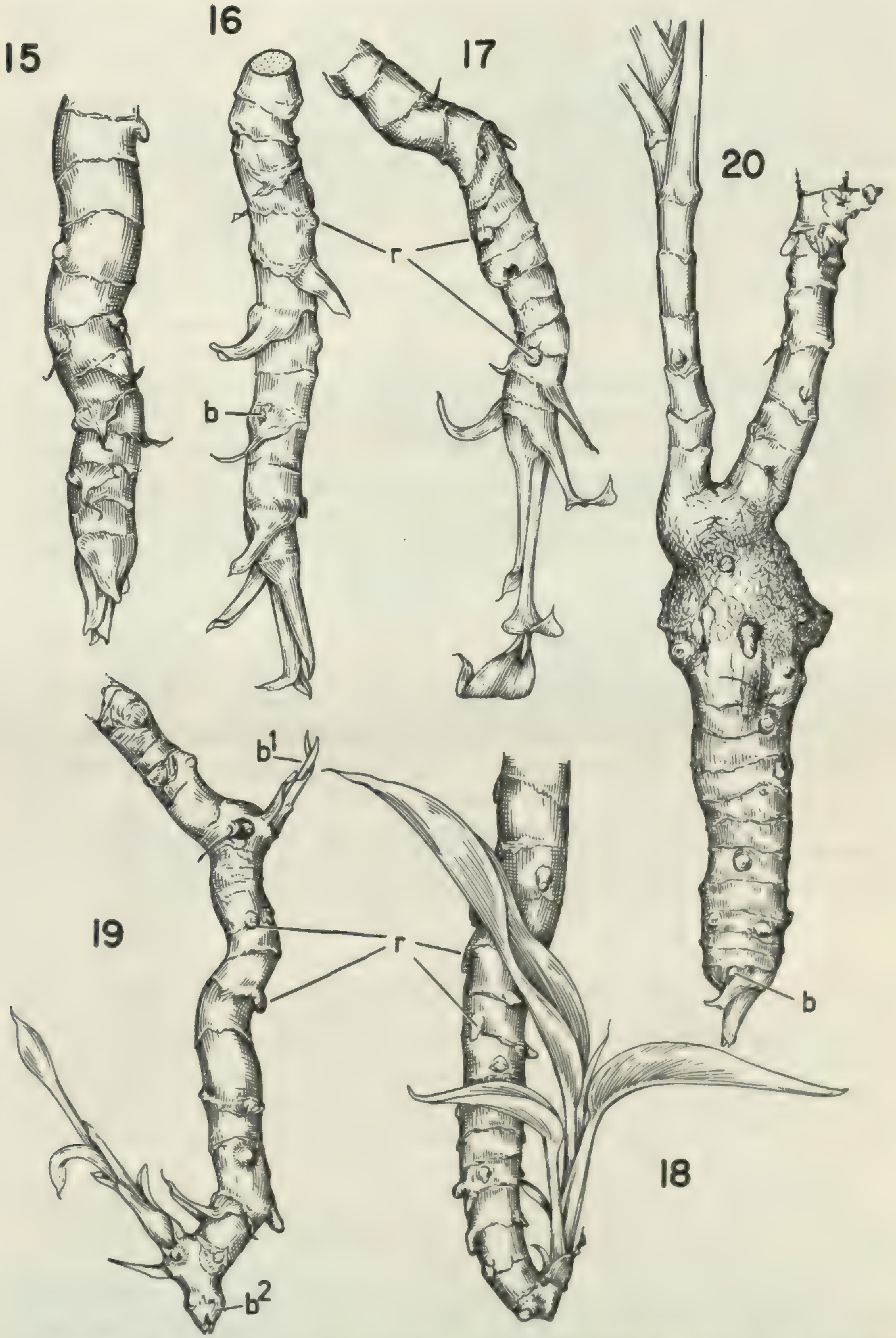
This type of shoot can, of course, also develop on the underground parts of mature plants, for example, as a branch of an existing rhizome. The seedling rhizome is therefore distinctive only because it occupies a particular place in the life cycle.

Aërial rhizomes are strictly positively geotropic, fleshy shoots which always originate from axillary buds, i.e. they occupy the same position as leafy shoots. However, they most usually originate from axillary buds either on the *lower* side of leaning branches or at the base of erect aërial shoots (FIGURE 7 K). They typically bear scale leaves which are spirodistichous, like the foliage leaves on erect shoots (Tomlinson & Fisher, 1971, p. 467). Like the erect shoots each scale leaf of the rhizome subtends a single axillary bud which is also strongly inhibited (e.g. FIGURE 16, b). Numerous root primordia are produced (FIGURES 16–19, r) but these remain as short initials which only develop further in a moist environment, as when the rhizome is buried. The range of leaf form on aërial rhizomes is considerable and varies from scales which are otherwise typical of underground rhizomes (FIGURE 15) to leaves which have a distinct lamina (FIGURES 16 and 17). The larger of these resemble the transitional leaves at the base of a branch which has developed from a dormant bud (cf. FIGURE 10 and FIGURES 16 and 17).

The apex of the rhizome itself may indeed turn upwards and develop into an erect leafy shoot, as shown in FIGURES 7 F and 18. Under these circumstances a new aërial rhizome usually develops from an axillary bud, either on the original rhizome (FIGURE 7 F) or on the leafy shoot into which the rhizome has been transformed (FIGURE 7 G). Specific examples of this are shown in FIGURE 19 (early stage) and FIGURE 20 (late stage). The leafy shoot into which the rhizome has become transformed may grow on to produce a typical flowering sympodium (FIGURE 7 G).

Underground rhizomes can also give rise directly to leafy shoots. This occurs when the axillary (or even apical) bud of an underground rhizome grows directly into a leafy shoot (FIGURE 7 H).

Aërial rhizomes may also "mimic" the pattern of branching of leafy shoots. Injured or decapitated aërial rhizomes may be substituted by new



FIGURES 15–20. **Cordyline terminalis,** aërial rhizomes, all × 1. 15, typical aërial rhizome with scale leaves; 16 and 17, the same, but with distal leaves developing incipient (FIGURE 16) or quite pronounced (FIGURE 17) blades; 18, aërial rhizome with distal end turning erect as a leafy shoot; 19, similar, but with a basal bud (b^1) initiating a leafy shoot, and a distal bud (b^2) ini-

lateral rhizomes which arise from distal buds (FIGURE 7 J). In uninjured, but long aërial rhizomes, proximal axillary buds often grow out as further rhizomes (FIGURE 7 I). The "mirror-image" relationship between leafy shoots and rhizomes is suggested in comparing FIGURE 7 C with 7 J and 7 E with 7 I. Unlike aërial shoots, however, in rhizomes there is no substitution growth associated with flowering since aërial rhizomes never become transformed directly into inflorescences (they may become so indirectly, as in FIGURE 7 G).

Peduncular branching. Both leafy and rhizomatous shoots can be developed at the base of the inflorescence, because the basal bract on the inflorescence subtends a bud which can grow out as a vegetative (FIGURE 25), rather than a reproductive (flowering) branch (FIGURE 24). Proliferation at this node may be complex, because of the development of buds subtended by the basal prophyll of the branch, whether it is vegetative or reproductive (FIGURE 26). This lower bract is always brought to the upper side by a characteristic twist of the base of the inflorescence axis. In this way the spirodistichous leaf arrangement of the shoot appears to be interrupted (FIGURE 8 A) although in fact it is continuous into the inflorescence. This "inflorescence" bud may grow out in a variety of ways, either as a leafy shoot (FIGURES 8 B, 21 and 22), or as an aërial rhizome (FIGURES 8 C; 23). Both a leafy shoot and an aërial rhizome may occur together (FIGURE 8 D) although one precedes the other.

It is significant that the base of the old inflorescence stalk retains only primary tissue, regardless of the amount of secondary tissue developed by the new vegetative shoot at its lowest node (FIGURE 23). Thus there is no secondary connection between the vascular tissue of the main axis (below the peduncle) and the new leafy shoot (above the peduncle). This is an observation with considerable developmental significance.

ANATOMY OF THE AXIS

Seedling. The underground seedling axis, both at early (FIGURES 3 and 4) and late (FIGURES 5 and 6) stages of development, never produces a cambium. There are usually 3 to 4 primary amphivasal bundles in the first internode and up to 8 to 9 bundles in the internode at soil level. These primary bundles are arranged in a ring and often are enclosed in an endodermis-like layer of sclerenchyma. The cambium is initiated first in the region of the axis at, or just above, soil level (as at internode X in FIGURE 4), and is active distally throughout the axis.

The seedling rhizome is produced from an axillary bud in this region where cambial activity is initiated (FIGURE 5, b). Vascular connection is

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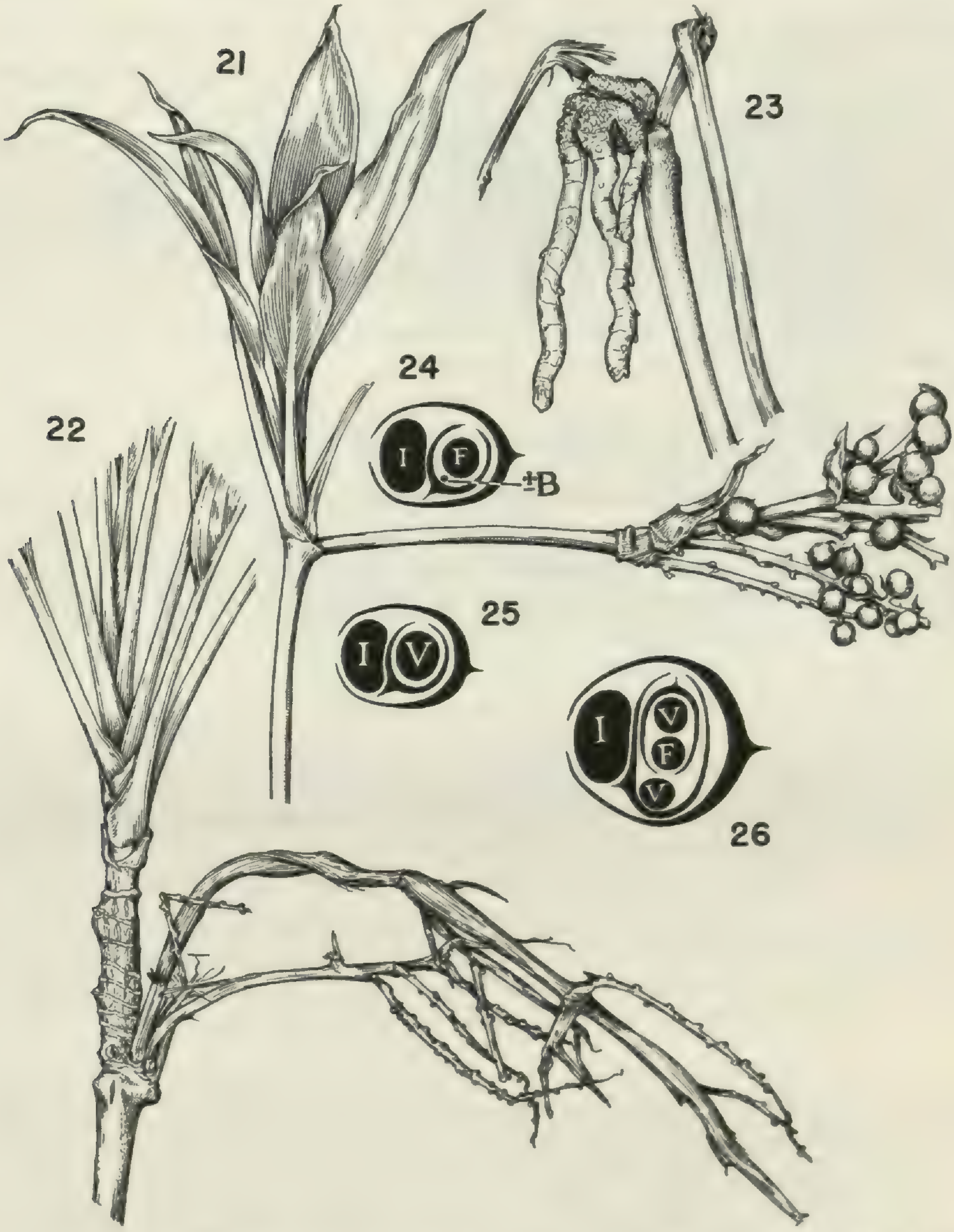
tiating a new aërial rhizome; 20, older stage with massive aërial branch rhizome (below) developed where a parent rhizome (upper left) has turned erect as a leafy shoot (upper right); b = dormant or developing buds; r = root primordia. A diagram corresponding to FIGURES 18–20 is given in FIGURE 7 F.



FIGURES 21–26. **Cordyline terminalis,** proliferating inflorescences, all × 1. *21*, vegetative branch developing as a leafy shoot, the simple example shown diagrammatically in FIGURE *25*; *22*, older stage of leafy shoot with abundant secondary tissue, the inflorescence axis below this still retaining only primary tissue; *23*, vegetative branch developing as a branching rhizome; *24*, diagram of first node of inflorescence, I = main axis; F = flowering branch; a bud (B) may or may not be subtended by the first leaf on the branch (prophyll) as shown; *25*, diagram of first node of inflorescence, proliferating vegetatively by replacement of flowering branch by vegetative branch (V), either a leafy shoot or a rhizome; *26*, diagram showing development of a flowering branch (F) and two vegetative branches (V) at the first node of a proliferating inflorescence, the two latter from buds both subtended by the prophyll; this probably accounts for the proliferation of several branches in FIGURES *22* and *23*, all seemingly from the same node. Habit diagrams corresponding to these specimens are: *21*, *22* = FIGURE 8 B; *23* = FIGURE 8 C.

established mainly by secondary tissues derived from the cambium which is continuous between both organs. At the soil surface (FIGURE 6) the anatomy of the axis is often intermediate between that of the rhizome and stem (as described below). If the junction of rhizome and stem is above the soil surface, the proximal region of the rhizome is stem-like. In older seedlings the junction of leafy shoot and rhizome is neither morphologically nor anatomically obvious since the tissue of the axis is secondary except for the few primary bundles of the original seedling axis.

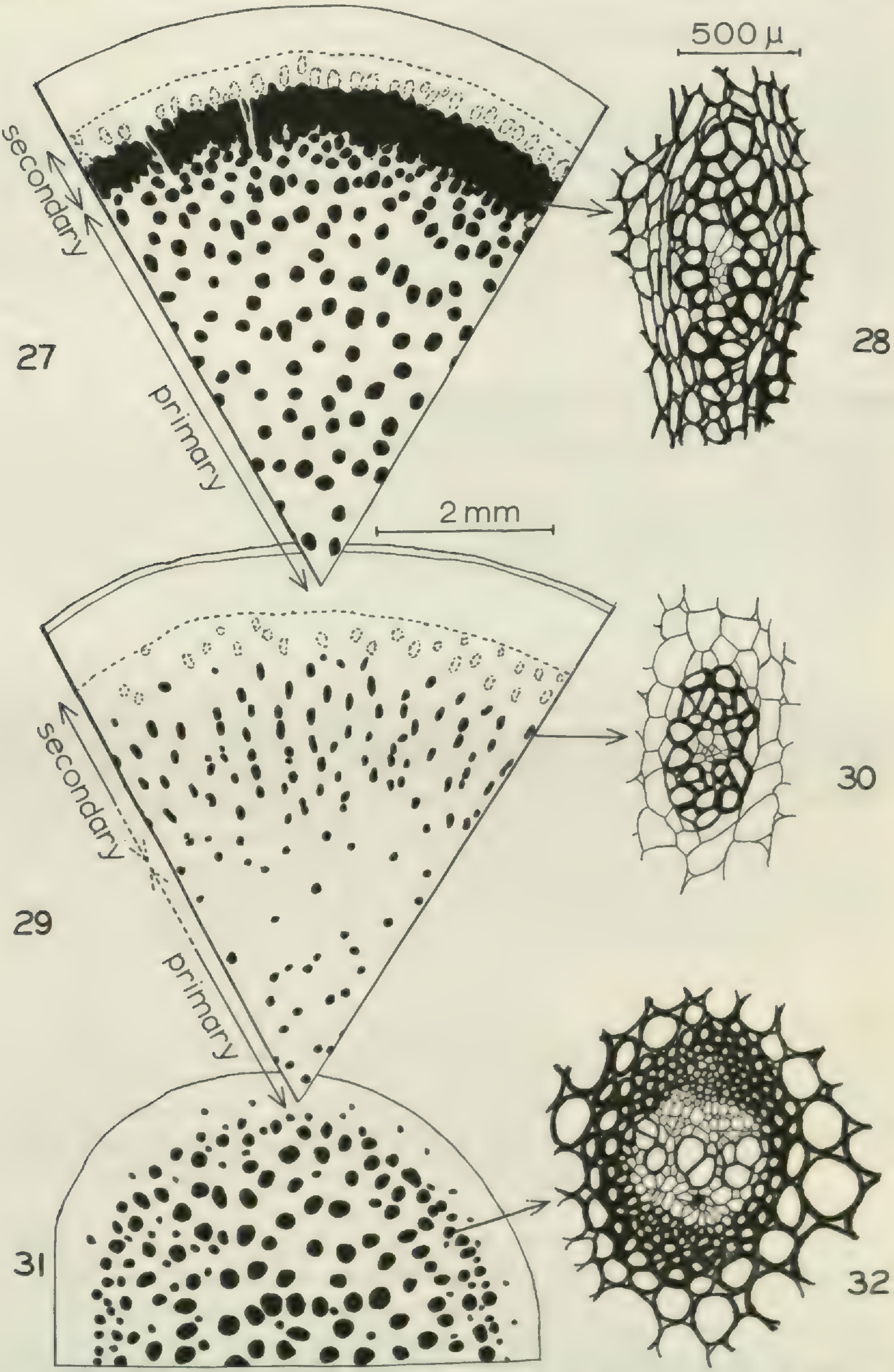
Adult axes. The anatomy of the three kinds of axis (leafy shoot; rhizome; inflorescence) is dissimilar and each may be described separately. The most distinctive feature of the inflorescence axis is that unlike the vegetative axes it never develops secondary vascular tissues.

(a) LEAFY SHOOT (FIGURES 27 and 28). In a mature leafy shoot with well-developed secondary tissues there is usually a sharp boundary between the primary zone, with thin-walled, unlignified and irregularly-arranged ground parenchyma cells, and the secondary zone, in which the ground tissues are radially arranged (reflecting their origin from the cambium) and with thick, lignified walls. There is little distinction between primary and secondary bundles because both are amphivasal. The sharpness of the boundary depends also on the amount of secondary establishment growth which the shoot may have undergone. The situation in *Cordyline* seems quite comparable to that in *Dracaena* which has been described in detail elsewhere (Zimmermann & Tomlinson, 1970).

The outer cortex is chlorenchymatous and the amount of secondary cortical tissue (if any) derived from the vascular cambium is difficult to establish, because cambial derivatives in this direction soon lose their radial alignment. Periderm (not developed in the stem from which FIGURE 27 was taken) is well developed in older parts of the axis.

(b) RHIZOME (FIGURES 29 and 30). Both underground and aërial rhizomes are similar in their internal structure, differing only in that the aërial rhizomes produce more periderm tissues and have a chlorenchymatous cortex. Secondary tissues are well developed in older rhizomes, but the vascular bundles are very diffuse (FIGURE 29). The boundary between primary and secondary tissue is indistinct because ground parenchyma in both regions remains unlignified. The secondary tissue, however, shows clear radial seriation of this parenchyma. Vascular bundles are again amphivasal, the secondary bundles being narrower than corresponding bundles in the leafy shoots (cf. FIGURES 28 and 30). The vascular cambium can be recognized much closer to the shoot apex in the rhizome compared with the leafy shoot, and this probably accounts for some of the differences between the two types of organ.

(c) INFLORESCENCE AXIS. This is strikingly different from the axis of the leafy shoot, of which it is a morphological extension, in that a vascular cambium is never developed (FIGURE 31). Most of the vascular bundles are collateral (FIGURE 32); they are narrower and more compact



FIGURES 27–32. **Cordyline terminalis,** camera lucida drawings illustrating anatomy of different kinds of axes in transverse section. 27, mature leafy shoot, boundary between primary and secondary tissue quite distinct; 28, detail of an boundary between primary and secondary tissue quite distinct; 29, mature aërial rhizome, boundary amphivasal secondary vascular bundle; 30, detail of an amphivasal between primary and secondary tissue indistinct; 31, mature inflorescence axis, no secondary vascular secondary vascular bundle; 32, detail of a collateral primary vascular bundle. tissue;

towards the periphery. Ground parenchyma cells have thickened and lignified walls.

When a vegetative axis arises on the inflorescence, as shown in FIGURES 22 and 23, the peduncle persists and produces a periderm, but never a vascular cambium. Inflorescences of comparable age, but without a vegetative branch, shrivel and die.

DISCUSSION

These observations on naturally grown specimens show that in *Cordyline terminalis* there is strict apical dominance of axillary buds. These buds, however, do have the potential for further extensive development. They may grow out as leafy shoots under circumstances which are quite comparable for other woody monocotyledons (Tomlinson & Zimmermann, 1969) and indeed seemingly for woody dicotyledons as well (Phillips, 1969; Smith & Wareing, 1964).

A unique property of these buds, however, compared with those in other genera of flowering plants is that they can develop as positively geotropic rhizomes in ways which "mimic" their development as leafy shoots. The rhizomes have the additional peculiarity of undergoing metamorphosis so that they can revert to negatively geotropic leafy shoots. It is therefore of interest to seek experimental evidence for possible hormonal mechanisms which control this divergent behavior. Future articles will present these experimental results which greatly clarify the situation and add to our knowledge of factors controlling shoot morphology in monocotyledons.

Additional information on initiation of secondary vascular tissues will attempt to explain the inability of the inflorescence axis to develop a vascular cambium even when it has proliferated a shoot with this ability.

SUMMARY

Cordyline terminalis has hypogeous seedling germination, unlike the epigeous germination of closely related species. Late seedling stages, however, show features diagnostic for the genus as a whole, with the development of a lateral rhizome which displaces the original seedling axis. Axillary buds are subjected to strong apical dominance, but have the potential to grow out as either negatively geotropic leafy shoots or positively geotropic, scale-bearing rhizomes. The latter can be transformed directly into the former. These different kinds of shoot expression seen on naturally grown individuals are described in detail. The value of this species as an experimental subject is emphasized. In outlining the distribution of secondary tissues in the various parts of the plant, the inability of the inflorescence axis to develop a vascular cambium is pointed out, a peculiarity which is particularly striking in parts which are below a vegetative proliferation. These observations provide a background for future experimental work.

ACKNOWLEDGMENTS

This study is part of a larger survey of the systematic and developmental anatomy of monocotyledons supported by N.S.F. grant GB–5762X, P. B. Tomlinson, Principal Investigator. We are indebted to the proprietor of Shaw's Nursery for access to specimens. Habit illustrations are by Miss Priscilla Fawcett, Botanical Illustrator at Fairchild Tropical Garden. Support for J. B. Fisher was provided by a fellowship from the Cabot Foundation, Harvard University.

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NOTES ON ASIATIC-POLYNESIAN-AUSTRALIAN SPECIES OF ERYTHRINA, II

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MY FIRST PAPER on this subject was published in 1939 (Preliminary Notes on Asiatic-Polynesian Species of *Erythrina*. Jour. Arnold Arb. **20**: 225–233. 1939) without the benefit of having studied specimens in European and Asiatic herbaria because of the war. Previously there was no compact treatment of the Asiatic-Polynesian-Australian species. Since that time I have examined specimens in several major European herbaria (BM, BR, E, G, K, L, P, S, U, Z) and as a result have made considerable progress in the understanding of several species. Six species (namely *E. glauca* Willdenow, *E. boninensis* Tuyama, *E. phlebocarpa* F. M. Bailey, *E. rostrata* Ridley, *E. sandwicensis* Degener, and *E. stipitata* Merrill) are here reduced to synonymy for the first time.

A conspectus of the species of *Erythrina* worldwide is in the course of preparation; in it I plan to give complete synonymy and type localities of valid species and synonyms, cite the type collections, give carefully compiled distribution, and discuss habit and habitat. In the present paper I am giving largely the information which I consider important or interesting and which it is not possible to include in the conspectus. Complete synonymy is given only for *E. variegata* L., but I am citing, of course, under other species those which are reduced to synonymy for the first time. Specimens are cited only for *E. microcarpa* Koorders & Valeton, *E. euodiphylla* Hasskarl, *E. merrilliana* Krukoff, and *E. insularis* F. M. Bailey which are very poorly represented in herbaria.

Of 13 species reviewed in this paper the chromosome numbers were published for seven (Phytologia **19**: 162, 163. 1969; Taxon **18**(3): 314. 1969; and Ann. Missouri Bot. Gard. **56**: 474. 1969). No counts have been published for *Erythrina microcarpa*, *E. resupinata*, *E. euodiphylla*, *E. merrilliana*, and *E. insularis*. A $2n$ number of 42 chromosomes was found in all Asiatic-Polynesian-Australian species sampled.

Three of the arboreous species under review (namely *E. arborescens*, *E. suberosa*, and *E. stricta*) and the herbaceous *E. resupinata* probably will prove to be frost tolerant in the Los Angeles area. It is kept in mind that by a formal proclamation on March 7, 1966, *Erythrina* was selected as the "Los Angeles official tree." *E. resupinata* will doubtless prove to be an excellent addition to rock gardens.

I wish to express obligation to Prof. Dr. C. G. G. J. van Steenis for his suggestions and help in obtaining certain critical type material. I am es-

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pecially indebted to Mr. R. Barneby for his assistance during the progress of this work, and for his cooperation in reading the manuscript.

Key to the Species [2]

1. Keel petals connate; seeds not red; rachises, pedicels, and leaflets (at least on petiolules and costa beneath) not stellate pubescent.
   2. *Standard long–stipitate, subrotund–rhombic*; pods ligneous; seeds opaque, umber to blackish with black markings. ..... 1. *E. fusca.*
   2. Standard and seeds not as above; pods follicular chartaceous (except in *E. arborescens*).
3. Keel petals subequal to wings; *pods seedless and indehiscent in the lower half.* ..... 2. *E. subumbrans.*
3. Keel petals conspicuously longer than wings; pods bearing seeds throughout.
   4. Plants native to Java. ..... 5. *E. microcarpa.*
   4. Plants not native to Java.
      5. *Perennial herbs with thickened roots* endemic to northern India. ..... 7. *E. resupinata.*
      5. Large trees.
         6. Pods ligneous; seeds shiny black; leaflets not ceriferous beneath; keel petals 1 1/3–2 times longer than wings. ..... 3. *E. arborescens.*
         6. Pods follicular, chartaceous; seeds isabelline to dark brown or sooty; leaflets ceriferous on both margins of veinlets beneath or intricately ceriferous beneath; keel petals 2 1/2 or more times longer than wings.
            7. Calyx campanulate; branchlets without numerous white spines when fresh. ..... 4. *E. suberosa.*
            7. Calyx subspathaceous; *branchlets heavily armed with white spines* when fresh. ..... 6. *E. stricta.*

1. Keel petals separate and subequal to wings (flowers of *E. insularis* not known); seeds scarlet-red or brownish red; rachises, pedicels, and leaflets (at least on petiolules and costa beneath) stellate pubescent.
   8. Seeds large (± 19 mm. long and ± 11 mm. broad), brownish red; pods with prominent veining; standard red. ..... 8. *E. variegata.*
   8. Seeds and pods not as above. Species keyed by geographic areas 9a, 9b, etc.

9a. Endemic to New Guinea; seeds scarlet with black hilum and with a black line extending from the hilum for approximately 2 mm. toward the chalazal end, 9–10 mm. long and 6–7 mm. broad; standard bright orange. ..... 11. *E. merrilliana.*

9b. Endemic to Australia.
   10. Seeds scarlet with white hilum, uniformly red, ± 13 mm. long and ± 7 mm. broad. ..... 13. *E. vespertilio.*
   10. Seeds scarlet with black hilum and with a black line extending from the hilum for approximately 2 mm. toward the chalazal end; 9.5–11 mm. long and 7–8 mm. broad; known only from the type collection from Turtle Island. ..... 12. *E. insularis.*

[2] Characters indicated by italics do not occur in other species.

9c. Endemic to Tahiti and Hawaii; standard orange; seeds ± 17 mm. long and 8 mm. broad. ..... 9. *E. tahitensis.*
9d. Endemic to Java; *all petals green; leaves fetid when fading.* .... 10. *E. euodiphylla.*

1. **Erythrina fusca** Loureiro, Fl. Cochinchinensis 427. 1790.

Erythrina glauca Willdenow, Ges. Nat. Freunde Berlin Neue Schr. 3: 428. 1801.

This species is a very large tree that thrives in a variety of conditions, but seems to prefer lowlands (seashores, swamps without outlets, low overflow lands, river banks, shores of lakes, etc.). In low swampy grounds where *Erythrina fusca* reaches especially huge dimensions, it often occurs in pure stands.

This is the most widespread species in the genus and the only one which occurs on three continents. It is undoubtedly dispersed by ocean currents.

In the Old World *Erythrina fusca* is found in a very extensive area, from Madagascar and the Mascarene Islands in the west; India, Burma, the Philippines and Carolines in the north; Samoa and Tonga Islands in the east; and New Caledonia, Papua, and Timor in the south.

In the New World it is found in the West Indies and on the Continent from Belize and Guatemala in the north to and including Peruvian, Brazilian, and Bolivian Amazonia in the south.

I did not place *Erythrina glauca* in synonymy in my monograph of the American species (Brittonia 3: 205–337. 1939) since before doing this I wanted to see *E. fusca*, as it appears in the Old World, in the field. There are no differences between *E. fusca* as it occurs in Asia, Polynesia, and Africa and as it is represented in the New World, in fact even its habitat is the same. According to a private communication from Prof. E. A. Bell and John Romeo of the University of Texas at Austin the alkaloids and amino acid patterns of seeds of this species, as it is represented in America and Asia, are very similar.

2. **Erythrina subumbrans** (Hasskarl) Merrill in Philip. Jour. Sci. Bot. 5: 113. 1910.

Plants of this species are medium size trees confined to low and middle elevations in light forests, open places, and secondary forests.

The species is found from southern India, Burma, Thailand, and Vietnam to and including Java, Borneo, and the Philippines.

3. **Erythrina arborescens** Roxburgh, Fl. Ind. 3: 256. 1832.

Erythrina moori Todaro, Hort. Bot. Panorm. 2: 7. *pl. 26.* 1879.

This species is composed of small to medium size trees, found at elevations between 1200 and 2100 meters. Leaves usually appear in May and fall off as soon as the tree has flowered in October.

Erythrina arborescens is found in India, Nepal, Burma, and China. In China it is the only species which is largely found to the north of the Tropic of Cancer (Sikang, Szechwan, Kweichow, and Yunnan).

In my previous paper (l.c.) I reported: "A doubtful species *Erythrina moori* was described on the basis of a cultivated plant of unknown origin and said probably to be from India. Examination of the original description and the plate establishes definitely the fact that it is an Asiatic rather than an American or African species. Examination of the type, if it exists, is necessary to check my conclusion that *Erythrina moori* is probably conspecific with *E. arborescens*."

Since that time I have become familiar with all known Asiatic and African species and there is no doubt in my mind that *E. moori* is a synonym of *E. arborescens*. The connate keel petals about 2 1/2 times longer than the wings, the ligneous pods with black seeds as shown on the excellent plate, are sufficient to establish its identity. In fact the black seeds are otherwise found only in three unrelated species of American *Leptorhizae*.

4. **Erythrina suberosa** Roxburgh, Fl. Ind. 3: 253. 1832.

This is a large deciduous tree confined to India (northern, central and southern), Nepal, Bhutan, Burma, Thailand, and Vietnam, ascending to 900 meters.

Without field studies and without seeing specimens in herbaria in India, it is not possible to decide whether *Erythrina glabrescens* (Prain) R. N. Parker (Indian Forester **46**: 647. 1920) should be placed in synonymy here or retained as a variety.

5. **Erythrina microcarpa** Koorders & Valeton, Booms. van Java 2: 61. 1895.

Erythrina stipitata Merrill, Philip. Jour. Sci. Bot. **5**: 112. 1910.

Erythrina microcarpa is a large tree, to 18 meters high, found in east Java along and near beaches on low elevations up to 900 meters.

Java: *Koorders Herbarium 46* (lvs) (L), *49* (lvs, flrs) (L), *50* (lvs) (L), *51* (lvs) (L), *65* (lvs, flrs) (K, L), *66* (lvs, flrs, frts, seeds) (K, L-lectotype), *71* (flrs) (L), *72* (lvs, flrs, frts, seeds) (K, L), *12785* (lvs, imm. flrs) (L), *14598* (flrs, imm. frts) (K, L), *14599* (lvs, flrs, imm. frts) (L); *Herb. Hort. Bot. Bogor 9620* (mixed coll., lvs-*E. subumbrans*, flrs-*E. microcarpa* (K, L); *coll. undesign. II/0–16* (1/VIII) (lvs, flrs, frts, seeds) (L); *Proefstation Java 837* (flrs) (L), *879* (flrs, frts) (L). **Philippines:** Lubang Island, near the town of Lubang, in open lands at sea level, *E. D. Merrill 958* (NY-isotype of *E. stipitata*); *s.n.* (lvs, flrs, frts) (K) with a note on the label "found without a ticket"; on the same sheet is mounted *A. D. Elmer 7132* (Jan. 1906) (lvs, flrs) from Island Leyte, prov. Leyte, loc. Palo — which is plainly *E. subumbrans*.

In the protologue of the species, Koorders & Valeton did not designate the type. It is proposed here to designate *Koorders Herb. 66* (L) as lectotype.

Examination of the two collections from the Philippines shows clearly that *E. stipitata* is conspecific with *Erythrina microcarpa*.

It will be noted that abundant material of the species from Java was distributed by S. H. Koorders in Europe only to Leiden and Kew; also that apparently only two sheets of *E. microcarpa* from the Philippines are available, as far as European and American herbaria are concerned. In the preparation of this paper I did not consult Asiatic herbaria.

The species is related to *Erythrina suberosa* and its relatives.

6. **Erythrina stricta** Roxburgh, Fl. Ind. 3: 251. 1832.

This species is a large deciduous tree usually aphyllous at anthesis. It is very spiny even in the context of its genus. The spines are white, a unique feature in the entire genus.

Erythrina stricta is found in India (northern, central and southern), Nepal, Burma, Thailand (where it is common in deciduous forests), Vietnam and China (eastern Tibet, southern Yunnan, and Kwangsi).

7. **Erythrina resupinata** Roxburgh, Fl. Ind. 3: 257. 1832.

This is an herb with a perennial thickened root which is in flower in April, at which time no part of the plant is visible but the raceme; the stem is formed later and is from 10 to 13 centimeters high.

This species is endemic to northern India.

Fruits and seeds of *Erythrina resupinata* were not seen by me in 1939. As is the case with the related species (namely *E. suberosa*, *E. microcarpa*, and also *E. stricta*), pods of it are follicular, chartaceous, not at all or slightly constricted between seeds, which are isabelline to dark brown or sooty. Seeds of the four species just mentioned are very similar. Those of *E. resupinata* are probably the smallest (8 mm. long and 6 mm. broad), followed by *E. microcarpa*; those of *E. suberosa* and *E. stricta* are larger, often 11 mm. long and 7 mm. broad.

Erythrina resupinata is very poorly represented in American and European herbaria.

Four American species of *Erythrina* (namely *E. leptorhiza* DC., *E. horrida* DC., and *E. montana* Rose & Standley confined to the higher elevations in Mexico, and *E. herbacea* L., as it occurs in the northern part of its range in the U.S.A.), as well as three species from Southwest Africa (*E. baumii* Harms, *E. mendesii* Torre and *E. pygmaea* Torre), although they are not related, are also herbaceous plants with thickened roots. Up to now no one appears to have studied the thickened roots of these species chemically. Such studies probably will prove to be of considerable interest.

This plant will likely be an excellent addition to rock gardens.

8. **Erythrina variegata** L. Herb. Amboin. 10. 1754; Amoen. Acad. 4: 122. 1759, based on *Gelala alba* Rumphius, Herb. Amboin. 2: 234, *t.* 77. 1750.

Erythrina corallodendrum L. var. *orientalis* L. Sp. Pl. 706. 1753, typified by *Mouricou* (Rheede, Hort. Malab. **6:** 13. *t. 7.* 1686). In the second edition of the *Species Plantarum* Linnaeus identified Rumphius's *Gelala litorea* Rumph. **2:** 230. *t. 76.* with Rheede's plant and cited it in synonymy.
Tetradapa javanorum Osbeck, Dagbock Ostind. Resa 93. 1757.
Erythrina picta L. Sp. Pl. ed. 2. 993. 1763, based on *Gelala alba* Rumphius Herb. Amboin. **2:** 234. *t. 77.* 1750.
Erythrina orientalis (L.) Murr. Comm. Götting. **8:** 35. *t. 1.* 1787.
Erythrina indica Lamarck, Encycl. **2:** 391. 1788.
Erythrina corallodendrum Loureiro, Fl. Cochinchinensis 427. 1790.
Erythrina spathacea DeCandolle, Prodr. **2:** 412. 1825.
Erythrina divaricata DeCandolle, *Ibid.* 414.
Erythrina lithosperma Blume, Cat. Gew. Buitenzorg 92. 1823 (nomen nudum); Hasskarl, Flora **25.** Beibl. II. 77. 1825, descr. and Pl. Jav. Rar. 381. 1848 (not *E. lithosperma* Miquel, Fl. Ind. Bat. **1:** 209. 1855).
Erythrina loureiri G. Don, Gen. Syst. **2:** 372. 1832 (based on *E. corallodendrum* Loureiro).
Erythrina carnea Blanco, Fl. Filip. 564. 1837; ed. 2. 393. 1845; ed. 3. **2:** 359. *t. 217.* 1879; not *E. carnea* Ait. Hort. Kew. **3:** 8. 1789.
Chirocalyx indicus (Lamarck) Walpers, Flora **36:** 148. 1853.
Chirocalyx pictus (L.) Walpers, *Ibid.*
Chirocalyx candolleanus Walpers, *Ibid.*
Chirocalyx divaricatus (DeCandolle) Walpers, *Ibid.*
Erythrina parcellii Bull, Gard. Chron. n.s. 1874 (II): 392, *fig. 82.* 1874.
Erythrina alba Cogniaux & Marchal, Plantes à feuillage ornamental **2:** *pl. 56.* 1874.
Erythrina marmorata Veitch ex Planchon, Fl. des Serres **23:** 21 (*pl. s.n.*). 1880.
Corallodendron divaricatum (DeCandolle) Kuntze, Rev. Gen. Pl. **1:** 172. 1891.
Corallodendron spathaceum (DeCandolle) Kuntze, *Ibid.* 173. 1891.
Corallodendron orientale (L.) Kuntze, *Ibid.* 172. 1891.
Erythrina phlebocarpa F. M. Bailey, Queensl. Agr. Jour. **1:** 368. 1897.
Erythrina variegata L. var. *orientalis* (L.) Merrill, Interp. Herb. Amboin. 276. 1917, and in Trans. Am. Phil. Soc. **24:** 208. 1935, based on *Erythrina corallodendrum* L. var. *orientalis* L. Sp. Pl. 706. 1753.
Erythrina mysorensis Gamble, Kew Bull. **1919:** 222. 1919.
Erythrina rostrata Ridley, Flora Malay Penins. **1:** 580. 1922.
Erythrina indica Lamarck var. *alba* Blatt. & Mill. in Jour. Bombay Nat. Hist. Soc. **33:** 628. 1929.
Erythrina boninensis Tuyama, Bot. Mag. Tokyo **49:** 373. 1935.
Erythrina variegata L. var. *orientalis* (L.) Merrill, forma *picta* (L.) Maheshwari, Bull. Bot. Surv. India **3:** 47. 1961.
Erythrina variegata L. var. *orientalis* (L.) Merrill, forma *parcellii* (Hort. ex Bull) Maheshwari, *Ibid.*
Erythrina variegata L. var. *orientalis* (L.) Merrill, forma *marmorata* (Hort. ex Veitch) Maheshwari, *Ibid.*
Erythrina variegata L. var. *orientalis* (L.) Merrill, forma *mysorensis* (Gamble) Maheshwari, *Ibid.*
Erythrina variegata L. var. *orientalis* (L.) Merrill, forma *orientalis* (L.) Maheshwari, *Ibid.* 48.
Erythrina variegata L. var. *orientalis* (L.) forma *alba* (Blatt. & Mill.) Maheshwari, *Ibid.*

Erythrina variegata L., *E. corallodendrum* L. var. *orientalis* L., and *E. picta* L. were based on plants from Herb. Amboin.; the type of *Tetradapa javanorum* is from Java; that of *E. carnea* Blanco from the Philippines; that of *E. corallodendrum* Loureiro from Vietnam; that of *E. indica* from India; that of *E. spathacea* from Santo Domingo. *E. divaricata* was based on a Sessé & Moçiño plate and was said to be a Mexican plant, but was doubtless drawn from a cultivated plant, probably collected in the West Indies. The type of *E. lithosperma* is from the Botanic Gardens, Bogor, Java; that of *E. parcellii* and of *E. alba* a cultivated (?) plant "from South Sea Island"; that of *E. marmorata* a plant of unknown origin "des îles de la mer du Sud"; that of *E. phlebocarpa* a plant cultivated in New South Wales, Australia; that of *E. mysorensis* from Mysore, South India; that of *E. rostrata* from Kedah, Malaya; and that of *E. boninensis* from the Island of Bonin.

DISTRIBUTION. Specimens were seen from the following countries: Tanzania (Tanganyika: Dar es Salaam & Mafia Island, Zanzibar), Madagascar, Maldive Islands, Ceylon, India (west Bengal, Mysore, Madras), Burma, Andamans, Thailand, Cambodia, Laos, Vietnam, China (Yunnan, Kwangtung, Hainan), Hongkong, Formosa, Ryukyu Islands, Malaya, Sumatra, Java, Timor, Borneo, Philippines, Celebes, Moluccas, New Guinea, New Britain, Solomon Islands, New Caledonia, New Hebrides, Fiji, Samoa, Tonga, Marianas, Carolines, Society Islands, Tahiti, and the Marquesas.

HABIT and HABITAT. This species is a large tree of the lowlands, being especially common along the sea coasts. It is now widely cultivated in the tropics; it was an early introduction to the New World and was even described twice as a new species, native to America, by DeCandolle.

In my previous paper (l.c.) I accepted the name *E. variegata* L. var. *orientalis* (L.) Merrill for this species, as suggested by E. D. Merrill. However, the arguments of A. A. Bullock (Kew Bull. 20: 294. 1966) are convincing and I now accept *Erythrina variegata* L. as the valid name for the species.

Erythrina parcellii and *E. alba* are obviously a form of the species with variegated leaves; I examined the specimen at Kew on which they were based.

The basis of *E. marmorata* is a sterile specimen of uncertain origin collected "des îles de la mer du Sud." It is obviously a horticultural form of the species with variegated (white-spotted) leaves.

Reexamination of the type-material of *E. phlebocarpa*, now mounted on three sheets (BRI) carefully annotated by S. T. Blake, shows that the protologue of this species was derived from elements of two species. The fruiting element (BRI 007963) represents *E. variegata* L., but the leaves associated with the pod by Bailey represent an African species, *E. lysistemon* Hutchinson. No flowers survive with the type-series as preserved at Brisbane, but the ostensible cotype at Kew has flowers of *E. variegata* mounted with foliage of *E. lysistemon*, whereas that at the British Mu-

seum (Nat. Hist.) has flowers and one pod of *E. variegata* mounted with leaves of *E. lysistemon.* In order to settle the synonymy, it is proposed here to designate the fruiting element, that part of the mixture which suggested the epithet *phlebocarpa* (BRI 007963), as lectotype. The name then falls into the synonymy of *E. variegata.*

It should be noticed that the flowers preserved at the British Museum and Kew cannot in any circumstances be considered part of the type-series for they disagree seriously with the original description. Bailey described the calyx of *Erythrina phlebocarpa* as "campanulate, oblique at the top," whereas the calyx of *E. variegata* is spathaceous, deeply split ventrally. It seems likely, therefore, that Bailey actually saw and described flowers of *E. lysistemon,* the species to which belong the leaves preserved at Brisbane, and that the flowers associated with leaves of *E. lysistemon* in the English herbaria were added as an afterthought, none of them, interestingly enough, being retained in Australia. My remarks on *E. phlebocarpa* (1939, p. 233) were based on study of the flowerless plants with associated pod and seeds now at Brisbane and flowers of an *Erythrina,* now recognized as the African *E. lysistemon,* which is extensively cultivated in Australian gardens.

The following material of the type collection of *E. phlebocarpa* was examined:

Australia. NEW SOUTH WALES: *Queensland Herb. 007961, 007962, 007963* (3 sheets deposited at Queensland Herbarium) (type coll. of *E. phlebocarpa,* lvs of *E. lysistemon* Hutchinson, and frts and seeds of *E. variegata* L.), the Kew sheet of the same collection consists of leaves of *E. lysistemon* and flowers of *E. variegata* L., whereas the British Museum sheet consists of leaves of *E. lysistemon* and one fruit and flowers of *E. variegata* L.

The following material of *E. lysistemon* from Australia was examined:

NEW SOUTH WALES: *Sabine Helms 1447* (flrs & mature lvs) (cult.) (US), *F. A. Rodway 813* (flrs) (Nowra, extensively planted in district, does not form fruit in this district — flowers fall as soon as they begin to grow) (K), *813A* (mature lvs) (K), *Kaspiev 396* (flrs) (G), *1308, 1318* (flrs) (Z).

QUEENSLAND: *C. T. White 9073* (flrs & mature lvs) (cult. Brisbane Bot. Gard.), *Brass 33486* (flrs & mature lvs) (Bromfield Crater, Atherton Tableland) (K), *Kaspiev 883* (flrs) (Z).

LORD HOWE ISLAND: *M. M. J. v. Balgooy 1109* (L) (flrs) (treelet c. 2 m., landslide of sand dune).

New Zealand. AUCKLAND: *W. R. Sykes 703/64* (flrs & young lvs, 30/9–1964) (Parnell Rose Garden) (CAS), *787/64* (flrs & young lvs, 2/10–1964) (Mt. Albert, exposed bank) (CAS), *697/64* (flrs & mature lvs, 29/9–1964) (Auckland Domain) (CAS), *700/64* (fl 30/9–1964) (Parnell Rose Garden) (CAS), *812/64* (frts, seeds & mature lvs, 3/10–1964) (Garden) (CAS); *Schweinfurth 1075* (flrs & lvs) (North Island, North Auckland) (M).

According to W. R. Sykes this species is known in cultivation in New Zealand as "*Erythrina indica* Lam." Seeds on his specimen are typical of *E. lysistemon* with black hilum.

On the basis of the original description of *Erythrina mysorensis* ("calyx spathaceous. . . . carinae petalae liberae") I suggested in my previous paper (l.c.) that *E. mysorensis* might be merely a related variety or a form of the common and widespread *E. variegata*.

In my previous paper (l.c.), I suggested that the doubtful *E. rostrata* may prove to be a synonym of the species. With the help of B. Verdcourt, I recently located the isotype of this species at Kew (*Ridley 15782*, April, 1890, from Kedah, Pulau Adang Seashore, Malaya). The specimen consists of young and mature leaves, 3 pods, and seeds. It manifestly belongs with the species.

I have examined the holotype of *E. boninensis* (*Takasi Tuyama s.n.* (TI) April 14, 1934, from the Island of Bonin, Chichijima, Omura). It consists of the upper portions of 4 rachises with flowers and a considerable number of loose flowers in poor condition. The flowers are rather small for the species but obviously belong here. I also examined 2 other sterile collections of *Erythrina* from Bonin *H. Hattori s.n.* (2/8–1905) (TI) and *Takasi Tuyama s.n.* (Dec. 24, 1968). They also are obviously of this species.

There seems to be no need to distinguish as species different forms of *Erythrina variegata*, and there is no justification for separation at the varietal level of *Gelala alba* Rumphius and *Gelala litorea* Rumphius. As early as 1917 Merrill stated: "Strictly, the specific name *variegata* should be adopted to include not only the form with the variegated leaves, but also the much commoner and widely distributed form with uniformly green leaves." It should be kept in mind, too, that forms with white flowers and/or variegated leaves occur also in other species (*E. berteroana*, *E. falcata*, and others).

Inasmuch as various species of *Erythrina* (especially *E. crista-galli* L., *E. lysistemon* Hutchinson, and *E. variegata* L.) were cultivated in greenhouses or in the open in Europe and the U.S., as well as on other continents for many years, there are many horticultural forms, some of which are referred to in the literature. I mentioned some of the horticultural forms of *E. crista-galli* in my monograph of the American species (Brittonia 3: 231. 1939).

C. A. Backer in 1911 (Schoolflora voor Java 1: 360) and then C. A. Backer & R. C. Bakhuizen van den Brink, Jr., in 1963 (Flora of Java, 1: 628) suggested that *Erythrina crassifolia* is probably a hybrid between what is now known as *E. variegata* and *E. subumbrans*. In the second publication, they give a rather complete description of *E. crassifolia*. It is cultivated locally in Java, its pods are usually poorly developed, and seeds are deformed or quite abortive, which is usually the case with *Erythrina* hybrids. I accept the suggestion that *E. crassifolia* is a hybrid without reservation, but I suggest that it is probably a hybrid between *E. variegata* and *E. fusca* (see for example *S. M. Popta 00527/96* (L) which has leaves closely resembling those of the latter species. Among other specimens of *E. crassifolia* I have examined *Koord. Herb. 76* (L) and *Herb. Hort. Bot. Bog. Kds. 32440* (L) marked as "n. sp." by Koorders.

9. **Erythrina tahitensis** Nadeau, Enum. Pl. Tahiti 80. 1873.

Erythrina sandwicensis Degener, Fl. Hawaii. 2: Fam. 169c. 1932.

This is a large tree, often found on arid rocky grounds including lava flows.

The species is found in Tahiti and Hawaii.

In a previous paper (l.c.) I stated: "I have seen *Nadeau 499* (type of *E. tahitensis*) deposited at Geneva. It consists of a single inflorescence with small flower buds, two flowers, one pod, one seed and no leaflets. From this available material it is impossible to decide whether or not this plant is specifically distinct from the plant native to Hawaii."

Recently I examined in Paris two additional sheets of this species, as it is represented in Tahiti. The holotype (*Nadeau 499*) consists of a fruiting inflorescence with 3 pods and seed, also one flowering inflorescence with immature flowers. Another collection (*M. Pancher 801* (1860), "sur montagne élevée des Tahiti) consists of a branchlet with two mature leaves and one immature, one flowering inflorescence, also one pod, and one flower in good condition. It is the basis of the name *E. montana* Forst. (Cuzent, G., Iles Tahiti 230. 1860).

I concluded that the Hawaiian plant is conspecific with the plant from Tahiti.

It was suggested that the plant is probably extinct in Tahiti. However, taking into account its habitat, this seems to be most unlikely. The type collection is from "precipicie, de Tâutana, 800 m"; for the habitat of the Pancher collection see above. Recently Brother Alain told me of his unsuccessful attempt to collect the very rare *E. buchii* Urban in the Dominican Republic where he saw it in flower on a precipice inaccessible without special climbing equipment. *E. tahitensis* is in flower in Tahiti in August, when collection is easier, as its striking orange flowers are visible at considerable distances. The native name for this species in Tahiti is "atae oviri."

10. **Erythrina euodiphylla** Hasskarl, Hort. Bogor. 178. 1858.

This is a large tree of the lowlands, including savannas with high grasses and scattered trees and shrubs.

It is endemic to eastern Java and neighboring Madura and Bali.

This species is represented in herbaria of Europe and U.S.A. only by the two specimens cited below:

Eastern Java: *M. Jacobs 4886* (L), *H. Zollinger 1440* (G).

This species is unique in the genus, having all petals green and leaves fetid when fading. The species is immediately distinguished from *Erythrina fusca*, *E. macrocarpa*, and *E. subumbrans* which also occur in Java, as its rachises, pedicels, and leaflets (at least on petiolules and costa beneath when young) are stellate pubescent. The only other species which is found in Java, *E. variegata*, is distinguished by the prominent veining on the pod and standards. The species is related to *E. stricta*.

I have not seen fruits and seeds of *Erythrina euodiphylla* as they are not available in European and America herbaria. However, immature fruit and seeds were described by Hasskarl.

11. **Erythrina merrilliana** Krukoff, Jour. Arnold Arb. 20: 227. 1939.

This is a striking tree with bright orange flowers which reaches the canopy in the rain forest on low elevations up to ± 1200 meters. Trees up to 24 meters high are recorded.

The species is endemic to New Guinea.

Since this species was described in 1939, seven additional collections were examined by me.

New Guinea. CENTRAL DISTRICT: *L. J. Brass 5265* (Mafubu, elev. ± 640 m.) (BM, NY-holotype), *Darbyshire 843* (Kairuku subdistrict, ± 5 1/2 km. north of Ikikina village) (L), *R. Schodde 2491* (near Karema, Brown River, elev. 30 m.) (G, K, L), *2642* (near southwest base of Mt. Lawes, elev. 30 m.) (G, L); MOROBE DISTRICT: *McVeigh & N. G. F. Ridgwell 7336* (Bulolo Valley, elev. 900 m.) (L), *B. Blackwood 270* (elev. 1200 m.) (K); MILNE BAY DISTRICT: *L. J. Brass 24251* (elev. ± 64 m.) (G, L). PAPUA: *C. E. Carr 12835* (Rouna) (BM).

Mature seeds were not seen at the time the species was described. Seeds are scarlet with black hilum 9 to 10 mm. long and 6 to 7 mm. broad and have a black line extending from the hilum for approximately 2 mm. toward the chalazal end. They are unlike those of any other Asiatic-Polynesian species but are indistinguishable from those of the Australian *Erythrina insularis*. Seeds of *E. merrilliana* resemble those of many African species (including *E. abyssinica* Lamarck) in being scarlet with a black hilum, and those of many American ones (including *E. berteroana* Urban) in having a black line extending from hilum about 2 mm. toward the chalazal end, although in none of the latter is the hilum itself black.

Beside *Erythrina merrilliana* two species have been recorded from New Guinea: *E. fusca* Loureiro and *E. variegata* L. The former has connate keel petals, a long-stipitate standard, and campanulate calyx; from the latter *E. merrilliana* is distinguished by its bright orange flowers and elliptic-oblong standard without prominent veining. This species is related to *E. tahitensis*. It is immediately distinguished, however, by the small seeds and by the calyx which in the part opposite the cleft has five long (up to 5 mm.) spurlike teeth, resembling in this character again certain African species.

12. **Erythrina insularis** F. M. Bailey, Queensl. Agr. Jour. 1: 228. 1897.

This is said to be a spreading tree about 4.5 to 6.5 meters high. It is known only from the type collection.

Australia. QUEENSLAND. Turtle Island: *F. M. Bailey 29* (June 1897), BRI-holotype — detached leaflets, petioles, fragments of branchlets, and a single

rachis with pods and seeds, BM — four leaflets and pods with seeds, K — three leaflets, rachis with pods and seeds (plus a pod of *E. variegata* L. mounted on the right).

This species is related to *Erythrina merrilliana*. It is stellate pubescent and its fruits and seeds are indistinguishable from those of the latter species (see under *E. merrilliana*).

13. **Erythrina vespertilio** Bentham in Mitch. Jour. Trop. Austr. 218. 1848.

This species is a short-boled tree, often from 0.3 to 0.9 meters in diameter and is rather common along the coastal areas of southern Queensland.

It is confined to tropical and subtropical Australia (Western Australia, Northern Territory, Queensland, and New South Wales).

The species shows extraordinary variations in the form of leaflets, to which Bentham (Fl. Austr. 2: 253. 1864) has already called attention. Two other species of *Erythrina* native to Africa, namely *E. livingstoniana* Baker and *E. humeana* Sprengel also show extraordinary variations in the form of the leaflets. They are not related to *E. vespertilio*.

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GEORGE B. HINTON, COLLECTOR OF PLANTS IN SOUTHWESTERN MEXICO

JAMES HINTON AND J. RZEDOWSKI *

AMONG THE PLANT COLLECTORS of Mexico during the Twentieth Century, George B. Hinton stands preëminent. Hinton was a metallurgist who decided at the age of fifty that his real and final interest lay in botany. During ten years of intense activity, from 1931 to 1941, he collected 16,300 numbers, concentrating his efforts in 26,000 square miles of the most inaccessible parts of the States of Guerrero, Michoacán, and Mexico. His botanical explorations, made on muleback in areas far beyond the railroads and the highways, in areas previously unvisited by other botanists, constitute a contribution to the knowledge of Mexican flora without recent parallel, not only because of the great numbers of new species and new genera he discovered, but also because of the geographical extension his collections provided for the ranges of thousands of species known from other localities or other states. It is estimated that at this writing, his collections include approximately three hundred and fifty new species and four new genera, while future studies of his material will undoubtedly produce even greater numbers of new species.

Hinton was born in London in 1882, one of four sons of Charles Howard Hinton, author and professor of mathematics, as well as a novelist; and of Mary Everest Boole, also a mathematician and author. Hinton was the grandson of George Boole, now known as the inventor of computer mathematics. He was a nephew of George Everest, Surveyor General of India, whose name was given to the world's highest mountain. He was also a nephew of Mrs. Voynich, author, and of James Hinton, surgeon and author.

In 1889, at the age of seven, Hinton left England, never to return; his family went to live in Japan, where his father was a professor of mathematics at the University of Tokyo. After seven years in Japan, the Hintons emigrated to the United States, where Charles Howard Hinton taught mathematics at Princeton, and later worked as a mathematician in the Patent Office in Washington, D.C.

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Until the age of fifteen, because of an extreme weakness of the eyes, Hinton's education was conducted by his mother and father at home. Thereafter Hinton attended various American universities, among which were the Minnesota School of Mines, Columbia University, the Arizona School of Mines, and the University of California at Berkeley. After the death of his father, Hinton paid not only his own way through college, but also that of his youngest brother Sebastian, by working during summers as an assayer in the mines of Mexico, which he probably first visited circa 1901.

In 1910, he married Emily Percival Wattley, who died in 1921, leaving him three sons, Howard, George, and James. When his children were grown he remarried twice, both marriages ending in divorce.

Once Hinton came to live permanently in Mexico, in 1911, he never left the country, not even temporarily during the worst of the revolutions. He was contemptuous of all those Mexicans and foreigners alike, who hastened out of the country at the first rebellion. He had come to live in Mexico for better or for worse, and there he stayed. Hinton loved Mexico and had a great affection for the people, especially the Indians and the peasants. in whose simplicity he found an echo of his own.

In the days when so many people despaired of the country's future, Hinton was one of the very few who kept the faith he had in the future of Mexico and its people.

Hinton worked in Mexico as an assayer, metallurgist, civil engineer, architect, industrialist, and finally as a botanical collector. During his apogee, he was considered the finest metallurgist ever to practice in Mexico, having solved problems which had defied the best metallurgical brains of the world for decades. He invented several important and widely used mining processes, as well as "Floating Cement," which was patented in Mexico, the U.S.A., England, Germany, and Sweden. A million dollar company had been organized to exploit his patent, when the collapse of Wall Street in 1929 obliged him to return to mining.

Hinton began his study of botany in 1931, as a hobby, first teaching himself the requisite Latin. In 1936, at the age of fifty-four, he retired from mining to dedicate himself full-time to his botanical explorations. In the early years of his botanical work, while still occupied with mining, he used as assistants Luis Martinez and Gerónimo Garcia. Upon retiring from mining, however, he enlisted the full-time coöperation of his youngest son, James, whom he sent to explore the remotest sierras of Guerrero and Michoacán. While he could ride horseback all day long, day after day, dismounting only to collect, an impaired heart prevented him from climbing mountains and cliffs on foot. Furthermore, a certain bronchial weakness prevented him from undertaking exploration of the highest sierras, where working and sleeping both cold and wet for days at a time was almost a condition of collecting at altitudes above three thousand meters.

The twenty-six thousand square miles where Hinton concentrated his explorations had remained botanically unknown for two main reasons, first, because of the banditry which had always, even to the present day,

characterized the area, and second because of the precipitous terrain, not only unpopulated, but virtually inaccessible.

The banditry obliged the collector to expose himself not only to great physical hardships but also to the possibility of loss of his life by assassination. While law and order had never been distinguished by their efficiency in the localities Hinton collected, a substantial portion of his work was done beyond their last outposts, where bandits and outlaws took refuge precisely because they were beyond the utmost reaches of the law. This hinterland of the great Guerrero and Michoacán sierras lay anywhere from one to seven days' journey by horse from the nearest agent of the law. The distance covered in a day's ride in this country, one of the most broken on earth, might be only five or ten miles, especially when barrancas over two thousand meters deep were encountered. But it was still a hard day's ride, or a hard day's walk. Botanical exploration took him as far as seven days on horseback from the nearest outpost of the Mexican Government, military garrison, post or telegraph office, and three days from the nearest human abode.

The only way of being allowed to work in such country, where many of the few inhabitants were outlaws, was to establish personal friendships with the people, and to live right in their huts, where the protection of their hospitality was of perhaps greater importance than the protection of their wattle walls or their leaky grass roofs. The first trip was the test, and Hinton had to arrive not alone but with a friend of his future host. Once under his roof, he was not only safe from his host but from the friends and companions of his host. Hinton then had to persuade his host to take him to the next hamlet or hut, and there present him with his following host, so that initially he was handed from one mountaineer to another, until he returned to civilization. Once the first shock of looking at a blonde and blue-eyed outlander was over, once the shock of fear and suspicion had been assuaged precisely by another of their kind, these mountain people were good friends to Hinton. He took presents to them and their children, and developed strong bonds of mutual respect and affection. He was so often implored to prescribe cures for their sicknesses, that little by little their plight caused him to overcome his extreme reluctance to prescribe medicine. He took with him such medicines as were most commonly needed, and gave them to his hosts, who received them with gratitude. When the nearest doctor, held in suspicious awe by the mountaineers, might be found only after a ride of several days, an effective remedy given by Hinton on the spot was never forgotten.

After the first trip Hinton came and went with impunity. Merchants, cattle buyers, missionaries, prospectors, and even soldiers often dared not enter the mountain fastnesses where Hinton came to feel more at home than in the towns and villages where his operations were based. Because they were not in any way participants of the feuds so numerous in the sierras, both Hinton and his son moved freely across areas infinitely wider than those permissible to the mountaineers themselves, who were locked into small localities by their fear of feuding enemies.

The second reason why those twenty-six thousand square miles had remained botanically unexplored was the nature of the country itself, broken, remote, without access other than by foot or by mule, and at the same time affording extremes of heat and cold without comforts or conveniences of any kind. Since he could not finance great caravans, Hinton had to live off the land, which often meant nothing but tortillas and salt, and sometimes plain hunger. For Hinton the privations of hunger and thirst, of barely passable living conditions, were of small account. Like the mountaineers, who chose freedom in the lawless mountains rather than the security of the village jails, Hinton chose freedom to explore the wild mountains rather than the comfort and the security of the cities where he might have lived well and long. Of his hosts he could ask for no more than what they themselves ate, and since they were so poor, their best food was often only corncakes and salt. While Hinton might enjoy good food and good liquor, he would permit neither to govern or influence his way of life. Although his explorations forced him to live for long periods on tortillas, with beans and cheese as an occasional luxury, his passion for collecting sustained him. These privations of diet were, of course, responsible for the acute anemia which, in part at least, was to cause his early death.

Since it was a financial and tactical impossibility to carry into the wilderness tents, furniture, or food, Hinton planned his expeditions to take advantage of every available hut or hamlet, where he might obtain shelter in which to prepare specimens, a place where he might obtain food not only for himself and his muleteer, but also corn and fodder for his animals. A typical shelter would be a one-room hut, with palm-thatch or grass roof, wattle walls, and too little space to accommodate the mountaineer, his wife and many children, let alone Hinton with his cot, his drying stove, and his gigantic tarpaulin specimen bags. The muleteer-assistant would sleep in the corn trough. During the dry season, of course, Hinton preferred to have his cot and his drying stove under a tree, thus avoiding the crowd in the hut. But in the tempestuous rains, he must crowd into the hut. Since there was usually no table available, Hinton used his tiny cot as a table for changing cardboards and packing specimens.

By using the lonely huts and the hamlets, Hinton relieved himself of the great difficulty of providing his own shelter and of preparing his own food. He would therefore stay in one hut or hamlet until he had thoroughly collected the vicinity, and then he would move to the next hut or hamlet, contriving of necessity to cover the distance between hamlets in a single day, however great that distance might be.

It was only the remotest mountains of the Sierra Madre del Sur which required camping out, and to these areas Hinton sent his son James, who made do using a pup tent now and then but who most often relied upon securing shelter in caves or under overhanging cliffs and often lay out the tremendous rainstorms under a riding cape, with the specimens well protected in their multi-layered tarpaulin bags. Riding through the rainstorms by day, James and the muleteer would strip naked, keeping their clothes

dry under the tarpaulin, and dressing again in these dry clothes once the storm had passed. For food they took "gordas," thick corncakes made with lard and cone sugar, which might last ten or fifteen days. Heated over glowing embers, these gordas were nutritious and not unpalatable. Monotony dissuaded gluttony, and, held to real hunger, a man could live two weeks at a time on a few kilos of gordas.

During his stay in the lonely huts of the sierras, Hinton could usually dispose of no more than a strip of seven or eight feet long by thirty inches in width, for both his cot and his stove, and this he must often dispute with dogs, sheep, chickens, cats, and pigs, all just as anxious as he to elude the icy driving rain. Quite often he must struggle with pigs or dogs scratching themselves or fighting ferociously under and over his cot, and from chickens defecating upon his cot from the rafters. Privacy was the one commodity that he sometimes really missed.

To the problem of exploring with an impaired heart the pathless solitudes of one of the most broken and mountainous areas in the world, Hinton replied with a superb saddle mule, the only item of expensive equipment that he permitted himself the luxury of using. His saddle mule, and his son's, were worth more than all the rest of their equipment combined. These saddle mules could not be bought with money alone. It was a question of money, luck, and skill. When a good saddle horse could be bought for fifty pesos, a fat cow for sixty pesos, and a pack mule for a hundred and fifty or two hundred pesos, Hinton had been offered as much as two thousand pesos for either one of the saddle mules. Pack mules they bought and sold every year, but the saddle mules they kept until they died. The first was Lenina, whom he bought in 1932, and who died in 1943. He gave Lenina to his son in 1937, when he bought Isabel, who died in 1956. His son James wrote to Dr. Carl Epling, asking that one of the twenty-six new Salvias she had helped discover be named after his saddle mule. Dr. Epling obliged by describing *Salvia leninae* Epl. Since a saddle mule was the pivot of Hinton's expeditions, she was lavished with every care. In planning an expedition, each day's journey must terminate where water and corn were available for the mules. If corn was not available, then it must be carried along, and whatever happened, the mules must have their corn at dawn and at dusk. When it came to finding food for himself and his muleteer, Hinton might give up late on a thunderstorming night. But until his mules had been fed, he would neither eat nor rest. An animal could not be denied, because, not knowing the reason, it felt only its hunger, but a man could bear his hunger because he knew the reason for it.

On an expedition, many stops must be made by the collector during the day, but the pack mules must go steadily on, else the journey would not be completed. The saddle mule must therefore be able to overtake the pack mules after long stops on the way, and to do this she must be a superb animal full of sinew and spirit, because the pack mules themselves had been carefully selected for speed and endurance. After each day's journey, Hinton's first preoccupation was for the mules, that after

they were fed and brushed, their backs must be carefully examined for the first sign of a crippling laceration. The eye could not be trusted to do the job, the fingers must feel the fur behind the withers, below the tail where the cruppers caught on the long downhills, and behind the forelegs where the cingle chafed on the upward steepnesses. Until the mules were fed and groomed, the men must abide their thirst and their hunger. Out in the wilderness, after eating their corn, the mules were let loose to forage for grass all night long. At dawn they would be back at the hut or the camp, squealing for their corn, which they loudly munched in nosebags while being carefully brushed and saddled and loaded. Each morning, in the lowlands, the mules must be scrupulously examined for the bite of a vampire bat, which, if neglected, would turn into a suppurating and sometimes crippling ulcer.

Such care did Hinton take of his animals that during ten years of using them to cover five or six thousand miles a year, no mount was ever lost. To this end a blacksmith was not entrusted to shoe his saddle mule, but he would shoe her himself, and during long expeditions, enough sets of new shoes were carried to reshoe his mule once every six weeks. Too often a blacksmith, if not watched closely as he worked, would save himself the hard work of paring down the hooves with the butteris and then rasping them down with a file, by chopping them down with a bolo, dumping the hooves as it is called, which results in destroying the animal's balance, often a question of life or death. Just as a nail driven into the quick may cripple a mule so can a dropped shoe. Aside from extra sets of shoes and nails, extra saddlepads and halters must be taken on an expedition for each mule.

Hinton had experimented with both horses and donkeys, but found that horses were too delicate and unreliable, while donkeys were not only too small for the deep river crossings and trails, but were cowed into utter helplessness by the incredibly fierce thunder and lightning storms which smote the mountains during the rainy season. Horses had too thin a skin, and no care was enough to prevent saddle sores caused by the excessive rocking of saddles on the broken terrain. Driven to utter exhaustion as might be necessary, they had not the mule's power of recuperation. Once burros or horses bogged down in a river or a swamp, they ceased to fight and resigned themselves to death. A mule, however, might be trusted to keep on struggling until she got out or killed herself trying.

While Hinton and his son were famed for their superb saddle mules, and while as a consequence they might ride farther and faster than the most knowledgeable of the mountaineers, this was the only good equipment they ever used. All other equipment must of necessity be cheap, because there was a strict limit to the amounts Hinton could subsidize with his small personal fortune. He was not able to afford good waterproof boots or leakproof riding capes, waterproof jackets, woolen socks, or adequate tents and sleeping bags. Neither he nor his son owned a pair of gloves. But if his life held many physical privations he was not even aware of them.

On various occasions prior to 1936, Hinton suspended his collecting for several months at a time because of the banditry. But this factor, which had been the real limiting factor to botanical exploration in the area he collected, was not a major problem for him. He had had so much experience with bandits during and after the revolution that he was confident of his ability to deal with any given situation. It was only when he had certain intuitive doubts about a group of robberies or assassinations that he stopped collecting the localities where these took place. That he had survived literally scores of bandit raids and scores of ransomings during the revolution did not seem to Hinton a matter of luck at all. He could always point out the glaring mistakes made by some one else who had been seriously wounded or had lost his life at the hands of bandits or rebels.

During his first years of exploring the remote sierras, Hinton reaffirmed the conclusion he had reached during the revolutions with respect to carrying firearms: that it was safer to go unarmed than to carry a gun. Not only did an unarmed person elicit less stranger-hostility from the mountaineers, but in a dangerous situation, he was forced to rely on his tact, on his skill, on his intelligence, and therefore he was safer than an armed man. A man's brain, used to the best advantage, was a better weapon than any firearm. A good weapon encouraged the folly of arrogance and pride. Moreover, in the lawless mountains, a pistol was one of the possessions most coveted by every man. If there were two things paramount in every man's mind, things for which he hungered, for which he sweated and strove, which completed him as a man and for which he might easily be provoked to assault or to kill, the first was precisely a good pistol or rifle. A good firearm put him on an equal footing with any man that lived. The second was a good saddle mule. Without these two possessions he was just any man. With them, he was a Don. With a good mule he was not only more able to defend himself against his enemies, known and unknown, but since anywhere he went, he must climb some of the steepest and roughest hills in the world, there was no greater convenience for him than a fine mule.

With their good mounts, Hinton felt that he and his son were already to a sufficient degree the objects of envy. It was unwise to compound the danger by carrying a good pistol. He finally compromised by carrying in his saddlebag a snub-nosed thirty-eight pistol, which he kept under his pillow at night. Upon one occasion, at a hamlet called Soyate, having been treated there with insulting harshness by the people, he strapped on his pistol openly, and required them to treat him civilly, which in future they did. However, when he moved to Aguililla, where every man carried a pistol and a cartridge belt, after the people had come to know and like him, they said to him, "In this country, it is the custom that every man should carry his good pistol. And if he does not carry one, then we take it amiss, and feel that he is a hypocrite, a man up to no good, a man to be mistrusted." Therefore Hinton said to his son, "When in Rome . . ." and in western Michoacán they carried pistols and cartridge belts openly.

In his house at Aguililla, Hinton kept his loaded pistol and cartridge belt hung from his bedpost, and he slept behind a locked door. The rise of banditry in 1940 led him to suspect that he might be taken for ransom, and he had as a young man been ransomed so often during the revolution that he had no patience for it now in his old age. If ever there should come a ransoming party for him, he said, he would shoot it out with them through the locked door, rather than submit to the nuisance of being ransomed again.

To a born naturalist like Hinton, the fears of the local inhabitants concerning wild animals brought only perennial surprise and amusement. The only creature to be feared, he often said, was another man. He could listen with fascinated pleasure at night to the roar of a jaguar nearby, while his muleteer cowered by the fire in horrified awe. Hinton knew that in his work as a collector, it was simply impossible that a jaguar would attack either him or his muleteer. It was even extremely unlikely that a jaguar or a mountain lion would attack his mules. And he lacked what was the native's worst fear of all — the fear of unknown, of imaginary beasts infinitely more terrifying than the jaguar, the puma, or the coral snake.

The dangers of being stung by scorpions or poisonous insects were ever present, but he had been stung so many times by scorpions that the stings were only a nuisance. What was to be really feared was an infected cut or scratch, especially in the lowlands, where scratches must be scrupulously treated and watched to avoid serious consequences. Another danger much greater than that of poisonous insects was the niguas, which, if given a chance, bored under the toe nails, spread over the sole of the foot, and in a month might cripple a man completely so that he would require massive surgery. This danger Hinton avoided by never touching the ground in the huts with his bare feet. In the lowlands, bedbugs, and in the highlands, fleas, required a man to sleep on a cot as long as he slept in a hut, else they would eat him alive.

The bite of a rattlesnake, or to a much lesser extent the bite of a coral snake, was a real and frequent danger, but to Hinton it was obvious that a man was much less likely to be killed by a rattlesnake in Guerrero than by an automobile upon a rare trip to Mexico City.

Diseases, from leprosy to typhus, from dysentery to spinal meningitis, were constantly encountered, but Hinton had a sublime confidence in his natural resistance to them. Moreover, there was often no choice. Once he had been in a hut for a few days and had come to the conclusion that his host had smallpox or typhoid fever, what could he do but refuse to be worried? He thought that as he had lived and worked in the Balsas River Valley, and had slept in the huts of families having pinto, from whose hands he received his tortillas, that sooner or later he would contract pinto himself. But did he not intend to live the rest of his life with the pintos anyway? And, after all, it was not a disease which incapacitated a man, it gave him only a startling complexion. Hinton's own frequent disease, malaria, he combated with prophylactic doses of 25 milligrams of quinine

sulphate a day. And the swarms of gnats and mosquitoes which pestered him in the lowlands, he combated felicitously with clouds of smoke from the cigars and cigarettes which he chain-smoked throughout his waking hours, both day and night.

It is, of course, one thing for a strong, healthy young man to bury himself in those wildernesses, and quite another thing for a man of later years, with an impaired heart and declining health. Every time he leaves the last railroad station, the last village, to ride into those solitudes, he is laying his life on the line. If he has put himself four or five days' ride from the nearest doctor, and six or seven days' ride from the nearest hospital, then any emergency of health may prove fatal, for he is far beyond medical help. When Hinton left the comforts of home and herbarium at Aguililla to explore the remote sierras, it was because he loved collecting as much as he loved his life. He was not only willing but quite literally eager to give his life to its pursuit.

In 1937, on the way to his herbarium at Los Placeres del Oro, he had an internal hemorrhage one night in Coyuca de Catalán, a hemorrhage he attributed to malaria. Passing and vomiting great quantities of blood all night, no doctor was to be found in all the village. He considered himself lucky in finding ice, which he ate until the bleeding stopped. He waited in Coyuca for a few days to regain his strength, and then rode on to Los Placeres del Oro, where he continued his work as if nothing had happened.

While Hinton was only too quick to point out that a man did not make his ancestors, yet certainly the accomplishments of his ancestors pressed him to think in terms not of immediate temporary gain but of lasting accomplishments. When he spoke of fame, as he rarely did, it was clear that his interest lay in being remembered only for having been of some lasting use to the world. There crowded upon him the work of so many ancestors who were remembered for their ideas, their books, their inventions, that he was driven to do things which he hoped would also be of permanent use to the world.

Having educated his family, and having acquired enough to live on for the rest of his life, Hinton could now devote himself full-time to the task which he loved above all others — plant collecting. Frequently, when he despaired of getting determinations from the specialists, when he saw this delay as a mounting obstacle to his work, he was tempted to get into taxonomy himself. But he would always realize that his greatest usefulness to Mexican botany lay not in taxonomy but in exploration. It was all very well to say that exploration could wait, that sooner or later, if he did not undertake it himself, some one else would. But no one knew better than he how swiftly the great forests were being destroyed by nomadic predatory farmers, who felled the great woods on the steep slopes, burned the pyre, planted a few handfuls of corn one or two years, and then, when the torrential tropical rains had denuded the slopes of their soil, moved deeper into the virgin wilderness. It was a job that had to be done now. By the time the area was crisscrossed with the roads that would bring in any and

all botanical collectors, the entire flora would have changed substantially and many of the species he was discovering would be lost forever.

At the end of ten years of botanical exploration, Hinton had inadvertently practiced so much medicine that he was contemplating a return to the University to become a titled doctor. There was such a crying need for medical knowledge everywhere he went, and he was so horrified by the witchcraft he saw practiced, that he had begun to think that if he was to continue to collect plants, if he was to continue to live at all, he must surely combine botany with medicine. That was the problem, to continue to live. He was under no illusions concerning his longevity. He came from a short-lived family, and he had lived a life full of hardships and privation. When he retired from mining in 1936, he often told those close to him that all he asked for was another five years of collecting plants. By 1943, he was indeed thankful for the eight years, and he did not know how he could live long enough to learn medicine. He could see himself breaking down physically, and when he died, he was satisfied that he had done as much as he could with his life. Feeling that in the future his work would be severely hampered by physical ills, he was not only ready but eager to die. Impatiently asking both doctor and nurse how much longer he must linger, he insisted that he could do no more, and his last words were that his work was done.

Hinton had the utmost confidence in the sure-footedness and intuition of his saddle mule, so that he rode down gorges and up precipices where only a mescal-crazed mountaineer would dare ride. When night found him still on the trail, he allowed his mule to find her way back to the hut, unworried and lost in his own thoughts. During a railroad accident, in which the train from Mexico City to Uruapan jumped a curve and rolled down an embankment, as Hinton lay recovering consciousness on the over-turned car, he heard something roll, and received a stunning blow on the hip. It was a castiron spittoon which had caught in the hat rack, and now rolled off and fell upon him. It broke his hip. But within six weeks he was not only out of plaster and out of the hospital; he was in the saddle collecting plants again, and anxious to forego travel by train.

During his last days, coming from Aguililla to Apatzingán, the truck he was riding in turned over, and he received a severe bruising which perhaps contributed to his death a few days later, from coronary thrombosis.

Hinton was unorthodox in much of his thinking. When he was collecting along the coast of Michoacán, below Coalcomán, in 1939, he was tracked down by a workman's commission from the Lane Rincón Mines. They delivered to him a petition signed by the 1200 workmen of the mine, who had received the mine from the company as payment of severance pay, back wages, and other legal benefits. They suspected that the mine had been sabotaged by the company, with the idea in mind that after a few months they would have to beg the company to come back and run the mine after the workmen had given up millions of pesos in benefits. Therefore Hinton left his beloved task of collecting plants in the twenty-six-thousand square miles of his garden and went back to the mine to help

his men. He found that the flotation mill had indeed been carefully and thoroughly sabotaged. However since he had himself built it, he had it running efficiently within a few weeks. And a few months later, he had the mine running at a profit. The grateful workmen not only rewarded him well, given their limited means, but made him a member of the union, Sindicato de Mineros, which at that time was so hated by both foreigners and upper class Mexicans alike. He used to show his union card to his friends at the British Club, remarking with delight that now he belonged to a "*real*" club.

To the physical problems of collecting in the mountain fastnesses on a limited budget, Hinton brought an inventiveness developed in engineering. What was needed was a system which would enable a collector to travel independently of a base for as long as three months, during which no new cardboards could be obtained, and during which all the specimens collected had to travel on the backs of two or three mules. Further, the specimens must be bright and crisp, and as impervious to moulding as quick thorough drying could make them. Hinton developed a drying furnace which could dry average plant specimens not with special blotters but with ordinary corrugated cardboards within twenty-four hours. First he designed several two-pack furnaces which he cached at strategic points in the sierras. Then he designed especially for his son a telescoping furnace, with a charcoal burner, and three compartments. The whole furnace, telescoped, formed only half a muleload. Set up, this model could handle two or three hundred specimens at a time. Quick drying not only retained the color of most leaves and flowers, but also permitted the preparation of excellent and beautiful specimens under the most difficult conditions. In addition it released cardboards for the next lot of plants. As paper folders became filled with specimens, these were tied into bundles, and the bundles forced into multilayered tarpaulin bags, which when properly tied resisted more than tempestuous rain storms of the Sierra Madre del Sur. They occasionally resisted the crossing of rivers when mules fell into unsuspected holes and had to flounder and swim their way out. These furnaces, had they required fuel from the outside, would have presented impossible requirements of weight and volume. But charcoal could be made anywhere and in any amount.

To Hinton, these were the happiest days of his life. He delighted in nature, and the idea that he could do something of small but lasting value for his adopted country and for botany filled him with satisfaction. He often commented that collecting plants satisfied the base instinct of acquisition and enriched science without exploiting anyone.

Hinton counted as a blessing each day that he could spend in the mountains, in sunlight, in cool shaded barrancas, on the sweltering plains, and under starry skies at night. Even the routine work of the herbarium, indoors, was not unpleasant to him. He said that as an amusement, handling the labels compared very favourably to playing cards, but was infinitely more useful.

When Hinton left mining to devote his full time to plant collecting, he

had to make a considerable adjustment in his relationship to those who worked for him. In mining he had been accustomed to nothing less than strict and immediate obedience to his orders. He had often had twelve or fifteen hundred men working for him. It usually did not take long for them to learn that here was a man who, while he might be exacting in command, was also uniquely and genuinely interested in their welfare.

While still at the Lane Rincón Mines, he had made an arrangement with the union for the company to provide an hour a day, and the men an hour of their own time, in order that the illiterate workmen should all learn how to read and write. For those who could read and write, he had set up classes so that electricians gave them lessons in electricity, mechanics in maintenance, carpenters in woodwork, etc., etc. He himself gave classes in metallurgy. It was understood that those who did not learn how to read and write within six months would be fired. Likewise, the literate must pass examinations in crafts and other skills. The result was that with the cooperation of the union, he was able to raise the level of skills and also of pay, because fewer and fewer men were able to do the same or more work.

But out in the lawless hinterland, he realized at once a very different problem: to use his own words, the unwillingness of the people to subject themselves to the indignity of being commanded by another for pay. Sympathetic with their pride and their freedom, he tried nevertheless to make use of the mountaineers but finally realized that it was simply impossible. They had not come upon a free life in order to work for a stranger, however unexacting the work. Therefore he used muleteers from the outside, and when they were not driving his mules from place to place, they helped him collect. This meant that he must often attend to all the routines himself, from collecting to drying and packing the specimens.

The first base that he used was El Rincón itself, from which he collected the District of Temascaltepec in the State of Mexico, and gradually extended his collecting southward to the Balsas River. During these years, from 1931 to the end of 1935, when he was becoming more and more intensely interested in the exploration, he collected on weekends and holidays, and had Martinez and Garcia collecting intermittently toward the Balsas, first from El Rincón itself, and then from substations at Tejupilco, Cutzamala, and Pungarabato.

As long as plant collecting was a part-time occupation for him, it was only natural that his main base should be at his house. El Rincón was very well situated for collecting the State of Mexico to which he devoted his collecting at the outset. Little by little, as he felt that the job neared completion, he extended his collections southward toward Guerrero.

Upon retiring from mining, he immediately moved his base to Los Placeres del Oro, Guerrero, which he chose, as he would choose subsequent bases, for the following reasons: First, because it was cheap, a factor of prime importance. Second, because Los Placeres was at the far edge of the area he had already collected, on the south side of the Balsas River and at the foot of the Sierra Madre del Sur, which he was to begin to collect.

The village had a postoffice, which was needed for mailing specimens, but beyond Los Placeres there was no outpost of law and order until the other side of the Sierra Madre, say, Petatlán, six days' ride away, on the Pacific Coast. From Los Placeres he collected for eighteen months, making one trip all the way to Atoyac de Alvarez, ninety kilometres west of Acapulco, an area which he afterwards entrusted to his son James.

From Los Placeres del Oro, the base was changed to Zitácuaro, Michoacán, a fifteen day trek with the entire herbarium packed into zinc cans and loaded on forty-eight burros. The trip was hard on the zinc cans, but for Hinton it was a leisurely trip with his son, more pleasant and cheaper than had he employed trucks, which he considered infinitely less reliable than burros. He had investigated prices in Zitácuaro, and found that they were attractive. What he wanted now was a base from which his son James could continue to make trips into the State of Guerrero, and from which he himself could make trips into western Michoacán.

Shortly after establishing the base at Zitácuaro, he established a substation at Coalcomán, Michoacán, whence he proceeded to collect westward to the coast, southward to Aguililla, while his son spent half a year collecting the area of Zitácuaro before resuming his trips to the Sierra Madre del Sur, with a substation at Atoyac de Alvarez, Guerrero. However, once the area of Zitácuaro had revealed excessive botanical similarity with Temascaltepec, Hinton found the base too far both for himself to collect western Michoacán and for his son to collect the Sierra Madre of Guerrero. Also, he felt the pressure of inflation in Zitácuaro. The last and final base was selected at Aguililla, Michoacán, which lay on no crossroads, and which, it might be said, lay at the end of the trail to nowhere. Like Placeres, it was the last outpost of law and order. (Once an outlaw crossed the Aguililla River, he would be pursued by no soldiers.) The village could be trusted to hold prices for some time, being at that time five days' ride beyond the nearest railroad or highway at Uruapan.

At Aguililla Hinton bought a house and store which he converted into a pleasant home and herbarium. He liked it so well that he planned to live there to the day he died. It was convenient for his exploration of the ranges between the hotland and the coast, as well as the coast of Michoacán itself. From there his son collected Mount Tancítaro, Michoacán.

Hinton had a respect for law which had no relationship to his personal opinion of a particular law. All his life he ran his businesses not as close to the margin of the law as he might, but rather as well within the law as he could. If a law was to a point senseless, Hinton did not chafe at it. He abided by it. He no more thought of violating the law than of falsifying scientific data.

During his time of collecting, and now also, it was the law that for each collection sent abroad one specimen must be deposited with an agency of the government. To comply with the law, Hinton began by taking duplicates of his early collections to the National Herbarium of the Instituto de Biología, a dependency of the Universidad Nacional Autónoma de México. Dr. Isaac Ochoterena, Director of the Instituto de Biología at

that time, refused Hinton's collections, first on the grounds that he had no room for them; and then on the grounds that he was not interested in Hinton's work, since there were already too many foreign names in Mexican botany. Actually, the Institute of Biology was not in any sense of the word a government agency, nor was there at the time any direct government agency to which Hinton might have presented his specimens. At Hinton's insistence, Dr. Ochoterena finally accepted a small number of Hinton specimens and gave both Hinton and his son letters designating them Honorary Collectors — letters which were certainly of considerable help with local authorities.

Thereafter, as his collections drew more and more attention abroad, and as Hinton realized their potential importance, he insisted more and more upon fulfilling his legal obligation by depositing one specimen of each of his collections in any government agency which might be induced to accept them, but to no avail.

In spite of his wishes, therefore, Hinton found himself in a position of being unable to comply with the law. This was a perennial source of worry, since it was obvious that his explorations might at any minute be stopped on the grounds that he was infringing the law. He tried therefore to obtain, for years, a letter from the Institute, in which they refused his offer of specimens, in order to be able to prove at any given time that he had tried without success to comply with the law. With the same insistence it refused his specimens, the Institute, with strict adherence to the law, denied him such a letter of corroboration.

Toward the end of 1939, several lots of specimens addressed to England, Switzerland and the U.S.A., were detained at the post office, and Hinton was required to produce a letter proving that he had deposited duplicate specimens with the government. Subsequently, he was informed that such a letter could now be obtained at the Instituto Biotécnico, a new department of the Ministry of Agriculture, (S.A.G.), and therefore a direct dependency of the federal government. To his great relief, Hinton found the Instituto agreeable to receiving a complete set of all his collections in return for a blanket permit to send his specimens abroad. Accordingly, the Instituto Biotécnico was presented with a set of nearly ten thousand specimens, and the lots at the post office were released. On the other hand, he was not given the blanket permit that he had been promised, nor were his specimens officially acknowledged. When his son went to the Instituto to recuperate the multiwalled tarpaulin bags in which the collection had been sent to the Instituto Biotécnico, he was appalled to find the bags half submerged in the water of a flooded cellar.

However, regardless of being denied his permit, he had no further trouble in shipping specimens abroad for another two years. During this period he continued to send a duplicate of everything he collected to the Instituto Biotécnico, which just as consistently refused to acknowledge them. In 1942, botanical parcels at the post office were once again seized, and Hinton was unable to obtain a permit in exchange for specimens

which he was equally unwilling to resort to smuggling or any other subterfuge to make the shipment.

His relationships with petty government officials in the provinces, say, on the level of village postmasters, garrison commanders, or municipal presidents were often marred by attempted impositions which he refused to tolerate. His work was frequently viewed with suspicious hostility. Actually, it could be stated in all truth that in Guerrero and Michoacán, a bandit-infested area, Hinton was more hindered by authorities than he was troubled by outlaws. It was a relief for him to ride beyond the last outpost of law and order, into the lawless and unexplored mountains, where the people went out of their way to help him because they admired him for his courage, respected him for his knowledge, and loved him for his generosity.

As far as could be done, Hinton used numeration chronologically. However, when two collectors worked simultaneously, especially during the four years his son collected for him, there would be one series of numbers available for his son collecting, say, in Teotepec, while he had another series of numbers for collecting, say, in Coalcomán. For this reason, numbers cannot be taken chronologically save in certain instances, when only one person was collecting at the time.

Hinton claimed to have acquired from his own father a strong collector's instinct, and had at various times in his life made serious and valuable collections, such as of metallic ores mounted on slides, orchids, and beetles. For many years he had collected orchids with his good friend Eric Ostlund, but he sold his orchid collection in 1929, when he went to live in Temascaltepec, and when his interest in plants became general. He collected beetles mainly for his son Howard, during the early 1930's. During other times he also collected sea shells and did some excavating for archeological objects. This latter field held great fascination for him, but he could never come to terms with its fundamentally illicit aspects, and therefore he abandoned it.

A major point of his satisfaction in living far beyond the last railroad or highway, of living life as it had been lived in the sixteenth and seventeenth century, was that he could enjoy its spiritual values, without being chafed by its lack of mechanical and material facilities. Hinton loved village life, with its definite but varied patterns, to the extent that he at last became a Catholic in order to partake more fully of Mexican village life. He had estimated that in Aguililla, the entire populace attended church once a day. When he was in the village, he loved to rise before dawn, bathe in a tub filled with cool water drawn by hand from a well, and then attend mass and come out from the church with the people in order to see the sun rise, to walk home slowly as the villagers went about their business, some on horseback to distant fields, some to the stalls to sell milk or to buy meat and fruit for the day, the blacksmith heating his forge, the merchant opening his store, the cowherd driving his cattle to pasture, and so on. He ate a simple breakfast of fresh milk, cheese, and tortillas topped off with hot black coffee from his own bushes.

Compared to the breakfasts he had out in the mountains, such a breakfast was luxurious to Hinton. Then he went into his herbarium and worked hard from seven to twelve, when he had a simple but to him luxurious lunch of broth, chicken stew, tortillas, Mexican rice, perhaps preceded by a cup of mescal and followed by black coffee. Then he slept until three o'clock and rose to spend another three or four hours in his herbarium. At night he supped on sweet bread with chocolate or coffee, and after taking a turn about the village square, retired early. In the village there were no professional people of any kind, except now and then a medical student doing his social service. His friends were the village craftsmen and the merchants, the graziers, and the mountaineers who came to visit him when he was at home and whose hospitality he was delighted to repay whenever he could.

He had felt the chill of patternless living in the cities, and now he basked in the warmth and charm of patterned living in the villages. That there was no electric light, no sewers, no refrigeration, and no communications bothered him not the slightest. He felt that the full daylight hours were ample for his work, and indeed they were, since there was no waste of time. He could visit the post office, the town hall, the church, the market, and be back in his herbarium within a few minutes. Not that he worked in haste. His pace was intense but unhurried. He enjoyed the dawns, the long slow days, the contented evenings, and the long quiet nights. He slept only a few hours, but spent long hours lying awake, rested, thinking and smoking while he awaited the coming of dawn. He enjoyed his friendship with the villagers, above all with the children, for whom he had swings built in his garden and often made little parties. He enjoyed having the time to consult his botanical works, of which he had a small but very good collection.

When the corn harvest failed in Aguililla in 1940, Hinton imported corn from the coast, and had it given to the children who came to ask for it. This he was able to do without incurring the hostility of the merchants who were speculating with high prices while he was giving it to those who could not pay such prices. During most of his time in the village, he gave English classes to those who wanted them and usually had a class of five or six adults to whom he gave an hour a day without charge. At the same time, while he hated to do it, he could not avoid prescribing medicine, principally to those who were too poor to buy the medicine or pay the doctor. His cures were so good that against his will he found himself obliged increasingly to prescribe for the most desperate cases.

In a financial sense, Hinton's big problem was not that his combined income from the theoretical sale of plants together with rent from houses could not cover the cost of exploring what he called his garden. During the four years that his son James assisted him full time, the sale of twelve specimens of each number, plus the income he had from his houses and other sources, would easily have paid for the cost of collecting. The problem was that he could not get determinations nearly as fast as he and his son could collect. The more determinations lagged, the more he had to

dig into his savings to finance the collecting, while his herbarium grew bigger and bigger. The additional specimens were a problem to collect and a problem to store. But the specimens in his herbarium could not pay the cost of collecting because they were increasingly undetermined. No more eloquent explanation of this point can be found than his letter to one of the herbaria responsible for determining his specimens, when he wrote in 1939: "You ask me to be patient about the determinations on the lots of plants sent you in 1934. *My mules have been eating corn for five years!*"

Once he had the collecting started, properly organized, he could hardly stop it. For one thing, he had the judgement to realize that his own lease on life would not wait. For another, he knew that his son could not continue to help him indefinitely. Therefore he must push the collecting NOW, regardless of determinations, regardless of the sale of specimens, trying to measure out his own personal fortune in proportion to his own life expectance, but preferring to gamble rather than to play it safe. Having started with the herbarium at Kew as the principal institution in classifying his specimens, the advent of the war obliged him to change to the Smithsonian Institution and the Gray Herbarium. Finally, at the time of his death, he had in many cases provided four or five specimens, and he still did not have the determination which would enable him to sell the remaining specimens, if any.

In 1941, the war brought botanical exploration to a close. Hinton left his herbarium to solve metallurgical problems at Taxco, with the intention of serving the cause in this manner for the duration of the war and not unmindful of repairing his financial position. His son James went to work for the Rubber Development Corporation. After a year at Taxco, when Hinton returned to Aguililla, it was to find that during his absence, the cyanide poisoning he had left in the herbarium had vanished, and the insects had attacked his collection with an astonishing rapacity. After going through the entire collection, a work of months, he calculated that something like thirty or forty thousand specimens had been lost. At a later date, after his death, the collection was again ravaged by insects and sustained another loss almost as great, after which his son removed it to Mexico City where the collection would be more frequently watched.

It might be said that the difference in what Hinton spent collecting and what he received from the sale of specimens, was determined rather precisely by the loss of specimens destroyed at one time or another by insects. Had all his specimens been determined and sold, the collection would have paid for itself through the sale of specimens.

During his expeditions, Hinton constantly shrugged off the lure of gold. Most of his collections were made in gold country, and he seldom visited a hut where his host did not show him a piece of gold-bearing ore, or perhaps a nugget, and try to inveigle him into developing a placer or a vein. Being a mining man, it was perhaps easier for him to refuse to touch a host of bonanzas, not only in gold, but also in silver, copper, lead, mercury, guano, precious woods, and cattle. He had not the time to become

rich, he had barely enough time to explore his wild and lonely garden. He was also often lured to visit other areas in other states by natives who knew fabled wildernesses. At first enthralled by their tales of the vegetation, he would finally shake his head and laugh and tell them that he had time to collect only one place well. He did not want to skim new species here and there, he wanted to establish a permanent record of everything that had once grown in his garden.

During the four years of most intense collecting, between 1936 and 1940, Hinton distributed his specimens as follows: one specimen of everything he collected to the Royal Botanic Gardens, Kew, the British Museum (Nat. Hist.), the herbaria at Zurich and Geneva, Harvard University, and the Smithsonian. Frequent lots were sent to the Field Museum and Missouri Botanical Garden, as well as to the New York Botanical Garden. Special groups, such as lupines and salvias, were sent also directly to Dr. Charles Piper Smith and Dr. Carl Epling. Infrequent sets of a thousand specimens were sent to Naturhistoriska Riksmuseum, Stockholm; Catholic University, Washington, D.C.; Mrs. Douglas of Mexico City, etc.

Hinton had originally made only two or three specimens of each collection. When the possibility of financing some of his expenses out of the sale of duplicates came to his attention, he began to take six specimens of each collection, wherever possible. When his son James returned from studies in Canada to devote himself full-time to assisting him, the number of specimens in each collection was increased to twelve, with the idea in mind of being able to finance future collecting. By this time, also, it was apparent that in order to have anything left for distribution, it was necessary to provide as many as three or even four specimens of each collection in order to obtain a determination without which the collection had little or no commercial value.

At the ratio of three specimens for a determination, if only six specimens were collected at the outset, then the price of fifteen U.S. cents per specimen for three specimens gave him 7 1/2 U.S. cents per specimen collected. However, if twelve specimens were collected at the outset, and three given for a determination, then in theory the gross return rose to 11 1/4 U.S. cents per specimen.

After Hinton's death in 1943, his son transferred some fifty-six thousand specimens to the New York Botanical Garden, which distributed these to forty-four herbaria listed on page 160.

There now remain in Hinton's collection approximately twenty thousand specimens.

It is estimated that the total number of specimens collected by Hinton, including those lost to insects and at government agencies, cannot exceed 150,000. Total remuneration received from the distribution of specimens, including subsidies from the Royal Botanic Gardens, Kew, is estimated at twelve thousand dollars. His records show that Hinton subsidized his collections to the amount of roughly another twelve thousand dollars — and, of course, worked without personal remuneration, other than the

enormous personal satisfaction, which he would not have traded for any money, full-time for five years, and part time for another five.

Because of his drying system, Hinton was able to produce very ample specimens, to the degree that Kew and others were often able to divide one specimen into several, and even this, sent to some other herbarium was again divided. As a consequence, Hinton's specimens found their way to a great many herbaria impossible to record in this work.

As his collecting progressed and determinations lagged more and more, he began to perceive that the bottleneck to increased knowledge of the Mexican flora was not so much botanical collecting as it was botanical determinations. To this end, he began to work on a mechanical device to reduce the task of determinations. This was a punching device, later perfected elsewhere, which he did not live long enough to build himself.

Hinton's interest in botanical collecting was principally scientific. If he could find only one or two specimens, he collected and sent them to the herbarium or to the specialist. This, naturally, deprived him of a specimen for his own collection, and it deprived him of specimens which could be sold. But this was for science, which was his main purpose. Furthermore, he had the means to indulge his pleasure in collecting. Had there been no scientific interest in his work, it would have destroyed his sense of mission, that sense of accomplishment which was so important to him. But he would still have enjoyed the work, the use of the faculties it demanded. He also enjoyed the work for its own sake, the exploration of barrancas and mountains which had perhaps never been looked upon by a trained eye backed by an academic education. He enjoyed riding horseback, the awaking long before dawn, the brushing, feeding, and saddling of the mules, and the early start so that the sunrise might be appreciated out in the woods or the top of the hills. Hinton loved the wilderness, and had it not been botany, some other mission would surely have taken him to those solitudes.

It was only when he could collect ten or twelve sheets that he had eight or ten for distribution to the herbaria. These, then, were to defray expenses. While there were rare times when expenses were fully met, his system of collecting meant, of course, not only that he and his son worked for many years without any personal income, but also that he used both the interest and the principle of a good part of his personal fortune. Had he brought to collecting a business attitude, and had he collected only the species which could have provided at the moment large, remunerative numbers of specimens, his work would have lost much of its botanical interest and value.

On the other hand, Hinton collected also the most common of species, in order to establish a record of distribution of known plants in botanically unknown areas. Without these numerous collections of common plants, the proportion of new species he collected would have increased spectacularly, but he would have lost the opportunity of extending the known geographical range of common as well as of new and rare species.

The more valuable he thought a specimen, the less he wanted it in his

own herbarium, where it would receive the least protection. In his arrangement with the different herbaria which worked upon his collections, Hinton supplied large numbers of additional specimens without cost. In the final outcome, a great many of the determinations he received cost him as many as four specimens, and even for this number, a very substantial portion of his collections had not been classified before his death.

Basically, the purpose of his work as Hinton saw it was to place before the specialist ample or at least adequate botanical material in the best possible condition. His attitude toward collecting was one of uncompromising honesty. When, as inevitably happens, there arose any confusion between a plant and its label, he destroyed both without hesitation, for if the main purpose of his collections was knowledge, then he could not possibly be instrumental in the fabrication of misbeliefs and errors. The purpose of his collections was indeed knowledge, and he was richly satisfied that in his own small way, he had served this purpose well.

Institutions to which duplicates of G. B. Hinton's collections were distributed by the New York Botanical Garden after Hinton's death. (See comments on page 158.)

NEW YORK BOTANICAL GARDEN
Bronx, New York.

SOUTHERN METHODIST UNIVERSITY
Dallas, Texas.

ACADEMY OF NATURAL SCIENCES OF PHILADELPHIA
Philadelphia, Pennsylvania.

UNIVERSITY OF WASHINGTON
Seattle, Washington.

U.S. DEPT. OF AGRICULTURE
Beltsville, Maryland.

ARNOLD ARBORETUM, HARVARD UNIVERSITY
Cambridge, Massachusetts.

UNIVERSITY OF CALIFORNIA
Berkeley, California.

UNIVERSITY OF MICHIGAN
Ann Arbor, Michigan.

UNIVERSITY OF ARIZONA
Tucson, Arizona.

MUSÉUM NATIONAL D'HISTOIRE NATURELLE
Paris, France.

TEXAS RESEARCH FOUNDATION
Renner, Texas.

UNIVERSITY OF TEXAS
Austin, Texas.

CONSERVATOIRE ET JARDIN BOTANIQUES
Geneva, Switzerland.

SCIENCE MUSEUM, THE INSTITUTE OF JAMAICA
Kingston, Jamaica.

RUTGERS UNIVERSITY
New Brunswick, New Jersey.

DUDLEY HERBARIUM
Stanford, California.

INSTITUTO MIGUEL LILLO
Tucuman, Argentina.

FIELD MUSEUM
Chicago, Illinois.

POMONA COLLEGE
Claremont, California.

NATURHISTORISKA RIKSMUSEUM
Stockholm, Sweden.

BOTANICAL MUSEUM AND HERBARIUM
Utrecht, Netherlands.

NATURHISTORISCHES MUSEUM
Vienna, Austria.

ROYAL BOTANIC GARDENS
Kew, Richmond, Surrey, England.

BOTANISCHES MUSEUM
Berlin-Dahlem, Germany.

MISSOURI BOTANICAL GARDEN
St. Louis, Missouri.

BOTANICAL MUSEUM, THE UNIVERSITY
Lund, Sweden.

BRITISH MUSEUM (NAT. HIST.)
London, England.

BOTANICAL MUSEUM AND HERBARIUM
Copenhagen, Denmark.

UNIVERSITY OF WYOMING
Laramie, Wyoming.

BOTANISCHE STAATSSAMMLUNG
Munich, Germany.

SMITHSONIAN INSTITUTION
Washington, D.C.

CORNELL UNIVERSITY
Ithaca, New York.

JARDIN BOTANIQUE
Leningrad, U.S.S.R.

JARDIN BOTANIQUE NATIONAL DE BELGIQUE
Brussels, Belgium.

BOTANICAL INSTITUTE OF THE ACADEMY OF SCIENCES OF THE U.S.S.R.
Leningrad, U.S.S.R.

UNIVERSITY OF ILLINOIS
Urbana, Illinois.

UNIVERSITY OF CALIFORNIA
Goleta, California.

WASHINGTON STATE UNIVERSITY
Pullman, Washington.

UNIVERSITY OF GEORGIA
Athens, Georgia.

UNIVERSITY OF MINNESOTA
Minneapolis, Minnesota.

IOWA STATE UNIVERSITY
Ames, Iowa.

UNIVERSITY OF OKLAHOMA
Norman, Oklahoma.

NATIONAL MUSEUM OF CANADA
Ottawa, Canada.

DUKE UNIVERSITY
Durham, North Carolina.

NOTE: Dr. Rzedowski has prepared with meticulous care as complete a list as possible of determinations of the Hinton collections. Completion of this task was made possible through the cooperation of Mr. C. V. Morton, of the Smithsonian Institution, who made available records compiled from his own and other institutions, and also by use of reports found in Hinton's files. The list of collection numbers (with or without names) is almost 500 pages long making it too costly to print, as well as unsuitable for the pages of a journal. Therefore, until the end of 1972, the editors of the *Journal of the Arnold Arboretum* will undertake to have prepared, at cost plus postage charges, xerox copies of the list for those individuals or institutions finding a copy important for proper use of their collections. Charges will be about $18.00 per complete list. — *Eds.*

PARTIAL LIST OF NEW TAXA BASED ON THE COLLECTIONS OF G. B. HINTON

GENERA

Hintonella Ames (Orchidaceae)
Hintonia Bullock (Rubiaceae)
Onocleopsis Ballard (Aspidiaceae)
Symplococarpon Airy-Shaw (Theaceae)

SPECIES AND VARIETIES

NOTE: The number following the name of the authority is the number of the type collection.

ACANTHACEAE

Aphelandra lineariloba Leonard, 3156
Beloperone longibracteata Leonard, 2159
Berginia hintonii Leonard, 5956
Buceragenia hirsuta Leonard, 5318
Carlowrightia coyucana Leonard, 6129
Carlowrightia lanceolata Leonard, 2672
Carlowrightia mucronata Leonard, 5533
Dicliptera aquatica Leonard, 3337
Jacobinia capitata Leonard, 1354
Pseuderanthemum axillare Leonard, 3200
Stenandrium mexicanum Leonard, 4292
Tetramerium hillii Happ, 5724
Tetramerium hintonii Happ, 3375

ANNONACEAE

Desmopsis mexicana Fries, 15836

APOCYNACEAE

Echites woodsoniana Monachino, 15325

ARISTOLOCHIACEAE

Aristolochia bullata Pfeifer, 14569
Aristolochia cardiantha Pfeifer, 9096
Aristolochia glossa Pfeifer, 15151

ASCLEPIADACEAE

Gonolobus megalocarpus P.G. Wilson, 7141
Matelea hintoniana Woodson, 1450
Pseudomarsdenia lanata P.G. Wilson, 7602

ASPIDIACEAE

Onocleopsis hintonii Ballard, 3297

BEGONIACEAE

Begonia asteroides Smith & Schub., 2206
Begonia cylindrata Smith & Schub., 5042
Begonia extranea Smith & Schub., 993
Begonia fernaldiana Smith & Schub., 9425
Begonia hintoniana Smith & Schub., 2050
Begonia michoacana Smith & Schub., 15186
Begonia nemoralis Smith & Schub., 15063

BIGNONIACEAE

Adenocalymma hintonii Sandw., 3784 [fl.] & 7259 [fr.]

BORAGINACEAE

Bourreria hintonii I.M. Johnst., 10866
Bourreria longiflora I.M. Johnst., 15908
Bourreria superba I.M. Johnst., 13834
Cordia coyucana I.M. Johnst., 8156
Cordia hintonii I.M. Johnst., 7740
Cordia subvelutina I.M. Johnst., 15066
Heliotropium cremnogenum I.M. Johnst., 8514
Heliotropium fallax var. *hintonii* I.M. Johnst., 3631

Heliotropium michoacanum I.M. Johnst., 15069

BROMELIACEAE

Catopsis mexicana L.B. Smith, 4692
Pitcairnia flexuosa L.B. Smith, 3948
Pitcairnia hintoniana L.B. Smith, 2040

BURSERACEAE

Bursera citronella McV. & Rzed., 12299
Bursera coyucensis Bullock, 6895
Bursera crenata P.G. Wilson, 12025
Bursera denticulata McV. & Rzed., 12021
Bursera dubia Bullock, 9349
Bursera fragrantissima Bullock, 9731
Bursera grandifolia f. *robusta* Bullock, 9774
Bursera heteresthes Bullock, 7812
Bursera hintonii Bullock, 6991
Bursera occulta McV. & Rzed., 12555
Bursera sarcopoda P.G. Wilson, 12293
Bursera sessiliflora var. *pubivalvis* Bullock, 9052
Bursera staphyleoides McV. & Rzed., 12073
Bursera trifoliolata Bullock, 6340
Bursera trimera Bullock, 6262
Bursera velutina Bullock, 6261
Bursera velutina var. *parvifolia* Bullock, 9193

CAMPANULACEAE

Diastatea expansa McV., 2644

CAPPARACEAE

Forchhammeria hintonii P.G. Wilson, 7617
Physostemon aureum R.C. Foster, 10537

CARYOPHYLLACEAE

Drymaria grandis Bullock, 5427

CELASTRACEAE

Euonymus corymbosus Sprague & Bullock, 325

COMPOSITAE

Bidens gracillima Sherff, 4546
Bidens minensis Sherff, 9453
Chaptalia hintonii Bullock, 3098
Coreocarpus hintonii Sherff, 9379
Cosmos hintonii Sherff, 10647
Cosmos purpureus var. *flavidiscus* Sherff, 1700
Dahlia hintonii Sorensen, 14499
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Dioscorea hintonii R. Knuth, 5215
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Collecting Localities of G. B. Hinton

The partial lists are arranged by districts (distritos), ancient administrative units, which were used by Hinton on his labels. Correspondence to modern municipalities (municipios) is indicated. The municipalities, access roads and coordinates were taken from modern maps and the position of a given locality on Hinton's original map may not coincide exactly with the corresponding listed coordinates. Altitude and vegetation data are taken from an archive of duplicate labels which was the main source of information in the elaboration of the list.

ESTADO DE MEXICO

District of Temascaltepec

Locality	Municipality	Approximate Coordinates		Altitude Meters	Access Roads	Predominant Forest Vegetation
		lat. n.	long. w.			
Acatitlán	Tejupilco	19°01′	100°19′	1130	Awdr * to Valle de Bravo and Tejupilco	Tropical
Anonas (Las Anonas)	Tejupilco	18°48′	100°22′	880	Awdr to Tejupilco and Bejucos	Oak
Bejucos	Tejupilco	18°47′	100°26′	610	Awdr to Tejupilco	
Berros (Cerro de los Berros)	Tejupilco	19°00′	100°05′	1950	Awdr to Temascaltepec and Tejupilco	Oak
Cajones	Texcalitlán	19°03′	99°53′	2460–2500 (2900?)	Awdr to Toluca and Sultepec	Oak-pine
Calera	Tejupilco	18°48′	100°24′	770	Awdr to Tejupilco and Bejucos	
Cañitas	Tejupilco	18°51′	100°18′	1000–1350	Awdr to Tejupilco and Bejucos	
Carboneras	Temascaltepec	19°03′	100°00′	1900–2030	Paved highway to Toluca and Temascaltepec	Oak-pine
Cerro de Los Berros (see Berros)						
Cerro Muñeca (see Ypericones)						
Chorrera	Tejupilco	18°55′	100°14′	1230	Awdr to Tejupilco and Bejucos?	Oak
Comunidad	Temascaltepec	19°08′	99°56′	2250–2750	Paved highway to Toluca and Temascaltepec	Pine-oak
Crucero (El Crucero)	Temascaltepec?	19°08′	99°50′	2670–3400	?	Fir-pine

Cruces (Las Cruces)	Temascaltepec	19°12′	99°53′	2900–3400	?	Fir-pine
Cucha	San Simón de Guerrero?	18°59′	99°59′	1960–2240	?	Pine-oak
Cuentla	Tejupilco	18°57′	100°02′	1960–2000	?	?
Cumbre (La Cumbre)	Texcaltitlán	19°02′	99°50′	2485–2950	Awdr to Toluca and Sultepec	Pine-oak-*Alnus*
Cumbre de Tejupilco	Tejupilco	18°57′	100°08′	1500–2000	?	Oak
El Crucero (see Crucero)						
Guayabal	Tejupilco	18°51′	100°18′	790	Awdr to Tejupilco and Bejucos	
Hornos (Los Hornos)	Temascaltepec	19°03′	99°56′	2500–2700	?	Pine-oak
Ipericones (see Ypericones)						
Ixtapan	Tejupilco	18°48′	100°09′	1000–1100	Awdr to Tejupilco and Amatepec	
La Cumbre (see Cumbre)						
Labor (La Labor)	Temascaltepec	19°02′	99°58′	1900–2100	?	Oak
La Sierrita (see Sierrita)						
Las Anonas (see Anonas)						
Las Cruces (see Cruces)						
Las Mesas (see Mesas)						
Las Vigas (see Vigas)						
Los Hornos (see Hornos)						
Limones	Tejupilco	18°50′	100°19′	(640?) 910–960	Awdr to Tejupilco and Bejucos	Oak
Luvianos	Tejupilco	18°55′	100°18′	1080–1450	Awdr to Tejupilco and Valle de Bravo	Oak
Mesas (Las Mesas)	Temascaltepec	19°01′	99°58′	2000	?	Oak
Mesón Viejo	Temascaltepec	19°10′	99°53′	2830–3300	Paved highway to Toluca and Temascaltepec	Pine-fir
Mina de Agua	Temascaltepec	19°00′	99°56′	1800–2000	?	Pine-oak
Nanchititla	Tejupilco	18°53′	100°28′	1100–1850	Awdr to Tejupilco	Pine-oak
Naranjo	Tejupilco	18°48′	100°25′	860	Awdr to Tejupilco and Bejucos	
Ocotepec	Tejupilco	18°52′	100°03′	1500		Oak-pine
Palmar (Palmar Chico)	Tejupilco	18°42′	100°24′	650	Awdr to Tejupilco	
Pantoja	Tejupilco	18°52′	100°01′	1500		Oak
Paso de Vigas (see Vigas)						
Peñón	Valle de Bravo?	19°08′	100°06′	1680–1960	?	?

* Awdr = All-weather dirt road.

ESTADO DE MEXICO

DISTRICT OF TEMASCALTEPEC

LOCALITY	MUNICIPALITY	APPROXIMATE COORDINATES LAT. N.	LONG. W.	ALTITUDE METERS	ACCESS ROADS	PREDOMINANT FOREST VEGETATION
Platanal	Tejupilco			?	?	Oak
Plaza de Gallos	Tejupilco	18°48′	100°18′	350–1200	?	
Puerto Salitre (see Salitre)						
Pungarancho	Tejupilco	18°53′	100°35′	950	?	Oak
Rincón	Temascaltepec	19°01′	99°58′	1930–2400	?	Oak-pine
Rincón del Carmen	Tejupilco	18°53′	100°08′	1340–1460	?	Oak
Salitre (Puerto Salitre)	Tejupilco	18°53′	100°17′	1300	Awdr to Tejupilco and Bejucos	Oak
San Lucas del Maíz				?	?	Pine-oak
San Miguel	Temascaltepec	19°08′	99°53′	2730–2770	?	Pine-fir
Sierrita (La Sierrita)	Texcalitlán	18°58′	99°55′	2200–2480	Awdr to Toluca and Sultepec	Oak-pine-*Alnus*
Socabón	Temascaltepec	19°02′	99°58′	2320	?	Oak-pine
Tejupilco	Tejupilco	18°55′	100°09′	1290–2000	Awdr to Temascaltepec and Valle de Bravo	Oak
Telpintla (Tempincla)	Valle de Bravo?	19°06′	100°04′	1800–1960	?	Oak
Temascaltepec	Temascaltepec	19°03′	100°02′	1700–2080	Paved highway to Toluca	Oak-pine
Tenayac	Zacazonapan?	19°04′	100°13′	1220–1720	?	Oak
Tequesquipan	Temascaltepec	19°04′	99°57′	2480–2800	Awdr to Comunidad	Oak-fir
Timbres	Valle de Bravo?			1660–1900	?	Oak
Tule	Valle de Bravo?			1500–1800	?	Oak
Vigas (Las Vigas, Paso de Vigas)	Tejupilco	18°55′	100°15′	1080–1300	Awdr to Tejupilco and Valle de Bravo	
Villaneda (Villa Neda)	Tejupilco			?	?	
Volcán (Volcán de Tejupilco)	Tejupilco	18°51′	100°09′	1380–1530	Awdr to Tejupilco and Amatepec	Oak
Ypericones (Ipericones includes Cerro Muñeca)	Tejupilco	18°48′	100°16′	1500–2300	?	Oak

SKETCH MAP
PLANT LOCALITIES
COLLECTED BY G.B. HINTON ET AL.
A COMPILATION OF THE BEST AVAILABLE DATA ADJUSTED WITH DIFFICULTY TO THE TOPOGRAPHY OF THE FIELD
SCALE 1 : 250 000
Drawn By G.B. Hinton Jr.
Date: 2/15/39
DISTRICTS
TEMASCALTEPEC 1
VALLE DE BRAVO 2
SULTEPEC 3
ZINACANTEPEC 4
MEXICO
MINA (COYUCA) 5
GALEANA 6
MONTES DE OCA 7
GUERRERO
ZITACUARO 8
HUETAMO 9
TACAMBARO 10
ARIO 11
URUAPAN 12
APATZINGAN 13
ARTEAGA 14
COALCOMAN 15
MICHOACAN
PACIFIC OCEAN
VOLCAN DE COLIMA
NEVADO DE TOLUCA
JALISCO
COLIMA
MICHOACAN
GUERRERO
MEXICO
URUAPAN
ARIO
TACAMBARO
APATZINGAN
COALCOMAN
ARTEAGA
HUETAMO
COYUCA
ZITACUARO
VALLE DE BRAVO
TEMASCALTEPEC
SULTEPEC
TOLUCA
TAXCO
ACAPULCO
RIO BALSAS
RIO TEPALCATEPEC
RIO GRANDE DE TEPALCATEPEC
RIO DEL MARQUEZ
RIO CHURUMUCO
RIO CUTZAMALA
RIO TUZANTLA
RIO PUNGARANCHO
RIO TEMASCALTEPEC
RIO CHILERO
RIO SAN FELIPE
RIO VERDE
RIO DE AMUCO
RIO DE LOS TRUCHES
RIO DE TEHUEHUETLA
RIO DE LOS BARRALES
RIO OTATLAN
RIO DE TECPAN
RIO SAN GERONIMO
RIO COYUCA
RIO GUAYAMEO
RIO SAN JOSE
RIO DEL ORO
RIO FRIO
RIO COAHUAYANA
RIO COYRA
RIO IXTALA
RIO SAN JOSE
RIO QUILALA
RIO HUAHUA
RIO TEPAME
RIO NEXPA
RIO CHUTA
RIO CARRIZAL
RIO DE LA HUIJULLO
FILO MAYOR
Cerro Teotepec
Zihuatanejo
Puerto San Jeronimo
Petatlan
Tecpan
Atoyac
Tejupilco
Pungarancho
Sn. Miguel Totolapan
Tlacotepec
Tlalchapa
Chapala
Tepalcatepec
Aguililla

GUERRERO

District of Galeana

Agua Escondida	Atoyac	17°30′	100°21′	1700–2200		Pine
Alcaparrosa	Tecpan	17°23′	100°57′	260–560		
Atoyac	Atoyac	17°12′	100°27′	0–660	Paved highway from Acapulco	
Camalote	Tecpan	17°25′	100°38′	250–500		
Carrizo (see Plan de Carrizo)						
El Plato (see Plato)						
El Reparo (see Reparo)						
El Verde (see Verde)						
Florida	Tecpan	17°31′	100°57′	760–880		Oak-pine
La Soledad (see Soledad)						
Mescaltepec	Atoyac	17°15′	100°23′	120–140		
Molino (Plan del Molino)	Atoyac	17°22′	100°23′	750–850		Oak-pine
Moreno	Tecpan	17°23′	100°36′	175–250		
Palo Solo	Tecpan	17°31′	100°40′	600		Oak
Pie de la Cuesta	Atoyac	17°28′	100°21′	1800–3000		Oak-pine
Piedra Ancha	Atoyac	17°30′	100°19′	2500–3150		Oak-pine
Plan de Carrizo (Carrizo)	Atoyac	17°23′	100°23′	550–1050		Oak-pine
Plato (El Plato)	Tecpan	17°35′	100°39′	800–1400		Oak
Puente del Rey	Atoyac	17°20′	100°16′	1000–1160		Oak-pine
Reparo (El Reparo)	Tecpan	17°22′	100°36′	75–100		
Río de las Selvas	Atoyac	17°27′	100°14′	2820		Pine
Río de Parotas	Atoyac	17°26′	100°14′			
Río de Santiago (Santiago)	Atoyac	17°14′	100°21′	680–700		
San Andrés	Atoyac	17°17′	100°19′			
San Juan de las Flores	Atoyac	17°17′	100°22′	380–620		
San Luis	Tecpan	17°16′	100°51′	0–140	Paved highway from Acapulco	
San Vicente	Atoyac	17°17′	100°18′			
Santiago (see Río de Santiago)						
Santo Domingo	Atoyac	17°27′	100°21′	850–1500		Pine
Sierrita	Tecpan	17°33′	100°37′	450–950		Oak-pine

GUERRERO

District of Galeana

Locality	Municipality	Approximate Coordinates lat. N.	long. W.	Altitude Meters	Access Roads	Predominant Forest Vegetation
Soledad (La Soledad)	Atoyac	17°17′	100°14′	1080		Oak-pine
Tecpan	Tecpan	17°13′	100°37′	20		
Teotepec	Atoyac	17°28′	100°10′	1800–3300	Awdr to Xochipala	Oak-pine
Toro Muerto	Atoyac	17°31′	100°16′			
Verde (El Verde)	Tecpan	17°16′	100°37′			

District of Bravos

Pueblo Viejo	Tlacotepec	17°31′	100°02′	2000		Oak
Puerto Hondo	Tlacotepec	17°31′	100°05′	2100		Pine

District of Mina (Coyuca)

Aguacate	Coyuca	18°07′	101°17′	1100		Oak
Aguazarca	Coyuca	18°07′	101°00′	1400–1760		Oak
Alacranes	Zirándaro	18°14′	101°07′			
Alborejo	Cutzamalá	18°40′	100°32′			
Ancón (El Ancón)	Coyuca	18°23′	100°41′			
Animas	Coyuca	18°22′	100°41′			
Anonas	Coyuca	18°20′	100°52′	200–360		
Arcelia	Arcelia	18°18′	100°16′		Paved highway to Iguala	
Armenia	Zirándaro	18°08′	101°19′	2000–2400		Oak-pine
Arrastras (Las Arrastras)	Totolapan	18°01′	100°18′	600		
Balderrama (see Valderrama)						
Barrales						
Bejuco (Rancho Bejucos)	Coyuca	18°12′	100°54′	400		
Brasiles (Braziles)	Coyuca	18°10′	100°52′	400		
Buenavista	Totolapan	17°46′	100°16′	1650–2275		Oak-pine

Calavera	Coyuca	18°11′	100°57′	450–1000		Oak-tropical
Camarón (Camerón)	Coyuca	18°13′	100°56′			
Campo Morado	Tlacotepec	17°35′	100°11′	900–2780		Oak-pine
Carriceras (Carrizera)	Coyuca	18°05′	101°05′	1000–1500		Oak
Carrizal	Ajuchitlán	17°36′	100°37′	1300–1750		Oak
Casas Viejas	Coyuca	18°01′	101°15′	1500–1640		Oak
Cayunche (see Cuayunche)						
Cerro Azul	Ajuchitlán	17°37′	100°39′	2250–2550		Oak-pine
Chacamerito	Ciudad Altamirano	18°18′	100°34′		Awdr to Ciudad Altamirano	
Chilacayote	Ajuchitlán	17°37′	100°38′	1450–1675		Oak-pine
Chirapitiro (see Zirapitiro)						
Chiriagua	Coyuca	17°54′	101°02′	1580–1860		Oak-pine
Cigarrillo	Coyuca	18°12′	100°55′	400–500		
Ciudad Altamirano	Ciudad Altamirano	18°21′	100°40′	400	Awdr to Iguala	
Coyuca (Coyuca de Catalán)	Coyuca	18°18′	100°41′	200–400	Awdr to Iguala	
Cruz Pacífica	Totolapan	17°33′	100°28′	2500–3050		Oak-pine
Cuahuilote (Cuajilote)	Cutzamalá	18°41′	100°32′	640		
Cuayunche (Cayunche)	Zirándaro	18°12′	101°11′	500		
Cuchara	Coyuca	18°06′	101°02′			Oak
Cuevas	Coyuca	18°05′	101°03′	1350		
Cuirio (Quirio)	Coyuca	18°18′	100°41′		Dirt road to Coyuca	
Cundán (Cundán Chico)	Coyuca	18°01′	101°08′	900–1320		Oak
Cutzamalá	Cutzamalá	18°27′	100°33′		Awdr to Ciudad Altamirano	
Diamantes	Coyuca	17°52′	101°00′	2320–2520		Oak-pine-fir
El Ancón (see Ancón)						
Espadines	Ajuchitlán	17°34′	100°37′	1500		
Espinazo del Diablo	Coyuca	18°04′	101°01′	1040–1400		Oak-pine
Filo Mayor	main crest of the Sierra Madre del Sur					
Fraguas	Tlapehuala	18°14′	100°29′		Awdr to Iguala and Coyuca	
Fresnos	Zirándaro	18°12′	101°17′	1260–2180		Oak-pine
Fundiciones	Coyuca	18°06′	100°59′			Oak
Guayameo	Zirándaro	18°17′	101°15′	560–900	Dirt road to Zirándaro	

GUERRERO

District of Mina (Coyuca)

Locality	Municipality	Approximate Coordinates		Altitude Meters	Access Roads	Predominant Forest Vegetation
		lat. N.	long. W.			
Idolo	Coyuca	18°03′	101°16′	1140		
Jaripo	Coyuca	18°18′	100°44′		Dirt road to Coyuca	
Jiotes (Jiotis)	Coyuca	18°06′	100°57′	500		
Juntas (Las Juntas)	Tlacotepec	17°34′	100°10′	1500		
La Soledad (see Soledad)						
Laguna	Zirándaro	18°18′	101°23′	1500–2500		Oak-pine
Lagunas	Zirándaro	18°09′	101°18′	1900		
Las Arrastras (see Arrastras)						
Las Juntas (see Juntas)						
Las Rosas (see Rosas)						
Llanos de Zacatlán (see Zacatlán)						
Los Barrales (see Barrales)						
Manchón	Coyuca	18°07′	100°59′	1100–1760		Oak
Manguito	Ajuchitlán	17°42′	100°38′	1500–1750		
Mesa Cuaxtle (Mesa Queisle)	Coyuca	18°03′	101°04′			
Mesa del Frijolar	Coyuca	18°03′	101°11′	1000–1140		Oak
Mono	Coyuca	18°02′	101°07′	800		
Nancintla	Totolapan	17°43′	100°13′	1460		Oak
Ojo de Agua	Cutzamalá	18°43′	101°30′			
Ojo de Agua	Coyuca	18°00′	101°15′	1500–1640		Oak
Otatlán	Totolapan	17°40′	100°13′	950–1550		Oak
Palma	Coyuca	18°03′	101°15′	1050–1100		
Paracho	Zirándaro	18°10′	101°23′	2300–2400		Pine-oak
Paraje Javalín	Totolapan	17°47′	100°16′	2000–2500		
Parancio	Coyuca	18°17′	100°52′	320		
Parotas	Coyuca	18°08′	100°58′	800		Oak

Paso de Arena	Coyuca	18°17′	100°50′		Dirt road to Coyuca	
Paso de San José	Cutzamalá	18°31′	100°33′		Dirt road to Cutzamalá	
Patambo	Coyuca	18°12′	100°51′	400–450		
Petlacala	Totolapan	17°47′	100°18′	1950–3000		Oak-pine
Pilas	Coyuca	17°51′	101°07′	1000–1660		Pine
Pino	Zirándaro	18°10′	101°05′	620–700		
Pinzán Morado	Coyuca	18°10′	100°53′	400		
Placeres (Placeres del Oro)	Coyuca	18°13′	100°53′	300–800	Dirt road to Coyuca	Oak-pine
Pochote	Cutzamalá	18°43′	101°29′			
Poleo	Zirándaro	18°17′	101°08′			
Poliutla (Policla)	Tlapehuala	18°15′	100°23′		Awdr to Iguala	
Puerto del Oro	Coyuca	18°16′	100°56′	400–800		
Puerto del Clarín	Zirándaro	18°12′	100°59′	750		
Puerto Rico	Ajuchitlán	17°38′	100°40′	1600–1850		Oak-pine
Puerto Suspiro	Zirándaro	18°07′	101°05′	1340		Oak
Pungarabato (see Ciudad Altamirano)						
Querendas	Ciudad Altamirano	18°20′	100°37′		Dirt road to Ciudad Altamirano	
Quirio (see Cuirio)						
Rancho Bejuco (see Bejuco)						
Río Frío	Coyuca	17°52′	101°05′	1260–2000		Pine
Rosario	Coyuca	18°25′	100°45′			
Rosas (Las Rosas)	Totolapan	17°40′	100°17′	1550–1600		
San José	Zirándaro	18°17′	100°58′	230–320		Oak
San Miguel	Coyuca	18°15′	100°37′			
San Nicolás (San Nicolás del Oro)	Totolapan	17°54′	100°15′			
San Pedro	Totolapan	17°40′	100°22′	1400–1600		
San Rafael	Zirándaro	18°12′	101°08′	800		
Santa Ana (see Santana)						
Santa Bárbara	Ciudad Altamirano	18°18′	100°38′			
Santa Rosa	Coyuca	18°18′	100°38′			

GUERRERO

District of Mina (Coyuca)

Locality	Municipality	Approximate Coordinates lat. N.	Approximate Coordinates long. W.	Altitude Meters	Access Roads	Predominant Forest Vegetation
Santa Teresa	Zirándaro	18°16′	101°05′	450–1040		Oak
Santana (Santa Ana)	Coyuca	18°04′	101°13′	1100–1350		Oak
Santo Domingo	Coyuca	18°23′	100°43′			
Sapo (Zapo)	Coyuca	17°55′	101°00′	740–860		
Soyate (Zoyate)	Zirándaro	18°09′	101°21′	2140–2400		Oak-pine
Suspiro (see Puerto Suspiro)						
Tanganhuato	Ciudad Altamirano	18°17′	100°35′			
Tario	Coyuca	18°25′	100°45′			
Tehuehuetla (Tejuejuetla)	Totolapan	17°48′	100°25′	1200		
Teotepec	Tlacotepec			1500–3600		Oak-pine-fir
Ticuiches (Tequeches)	Zirándaro	18°14′	101°18′	1650–1880		Oak-pine
Tierras Blancas	Coyuca	18°09′	101°17′	1400–1800		Oak
Timbre	Coyuca	18°15′	100°52′	400		
Tinajas	Coyuca	18°21′	100°41′			
Toro Muerto	Totolapan	18°31′	100°16′	1800–2900		Oak-pine
Totolapan (San Miguel Totolapan)	Totolapan	18°01′	100°18′	600		
Trincheras	Coyuca	18°05′	101°16′	1200–1300		
Truchas	Cutzamalá	18°44′	100°28′		Dirt road to Cutzamalá	
Vacas	Coyuca	18°04′	101°10′			
Valderrama (Balderrama)	Cutzamalá	18°43′	100°31′		Dirt road to Cutzamalá	
Vetarrón	Cutzamalá	18°43′	100°29′		Dirt road to Cutzamalá	
Vinatita	Coyuca	18°06′	101°16′	1250		
Yesqueros (Yesceros)	Totolapan	17°47′	100°29′	1600–2250		Oak-pine
Zacatlán (Llanos de Zacatlán)	Coyuca	18°05′	101°07′	1500		
Zapo (see Sapo)						
Zihuaquio (Zihuagio)	Coyuca	18°02′	101°14′	1050–1100		Oak

Zirandarangio	Coyuca	18°20′	100°41′			
Zirapitiro (Chirapitiro)	Cutzamalá	18°35′	100°33′		Dirt road to Cutzamalá	
Zoyate (see Soyate)						
			DISTRICT OF MONTES DE OCA			
Balcón	Petatlán	17°51′	101°11′	560–720		
Banco	Petatlán	17°37′	101°02′	560–800		Oak
Buenos Aires	La Unión	17°56′	101°15′			Oak-pine
Capirial	Petatlán	17°47′	101°17′	840–960		
Carboneras	La Unión	18°01′	101°19′	1150–1400		Oak
Ciruelo (Ciruelos)	La Unión	17°53′	101°21′			
Filo Mayor	main crest of the Sierra Madre del Sur					
Guadalupe (Mineral de Guadalupe, Real de Guadalupe)	La Unión	17°59′	101°18′	900–1200		Oak
Mameyal	Petatlán	17°35′	100°59′	700		
Murga	Petatlán	17°39′	101°17′	100		
Pasión	Petatlán	17°38′	101°06′	400–1000		Oak-pine
Petatlán	Petatlán	17°31′	101°16′	100	Paved highway to Acapulco	
Pilas	Coyuca(?)	17°49′	101°07′	2100		
San Antonio	La Unión	17°57′	101°17′	800–1040		Oak
Soledad (Soledad Palma)	Petatlán	17°50′	101°08′	720		Oak-pine
Tusal (Tuzal)	Petatlán	17°26′	101°15′	0	Paved highway to Acapulco	
Vallecitos	La Unión	17°55′	101°19′	400–760		Oak-pine
			MICHOACAN			
			DISTRICT OF APATZINGAN			
Acahuato	Apatzingán	19°10′	102°20′	800–1400		Pine
Aguaje	Tepalcatepec	19°00′	102°43′	200–350	Awdr to Apatzingán	Thorn
Aguililla	Aguililla	18°44′	102°47′	800–1100	Awdr to Apatzingán	
Apatzingán	Apatzingán	19°04′	102°22′	300–400	Paved highway to Uruapan	Thorn
Buenavista	Buenavista	19°12′	102°33′	400–800	Awdr to Apatzingán	Tropical-thorn

MICHOACAN

DISTRICT OF APATZINGAN [cont.]

LOCALITY	MUNICIPALITY	APPROXIMATE COORDINATES LAT. N.	LONG. W.	ALTITUDE METERS	ACCESS ROADS	PREDOMINANT FOREST VEGETATION
Rancho Viejo	Buenavista	19°12′	102°40′	700	Awdr to Apatzingán	Tropical-thorn
Tepalcatepec	Tepalcatepec	19°11′	102°50′	300–400	Awdr to Apatzingán	Tropical-thorn
Tiquiluca	Tepalcatepec			700	Awdr to Apatzingán	Tropical
DISTRICT OF URUAPAN						
Tancítaro	Tancítaro			1600–3900		Oak-pine-fir
DISTRICT OF COALCOMAN						
Aquila	Aquila	18°37′	103°30′	50–250	Awdr to Tecomán, Col.	Tropical
Barroloso				1300–2900		Oak-pine-fir
Chacalapa				150–250		Tropical
Coalcomán	Coalcomán	18°46′	103°09′	1000–1250	Awdr to Apatzingán	Oak-pine
Huizontla	Villa Victoria	18°09′	103°24′	350–1050		Oak & tropical
Ocorta	Coalcomán	18°36′	103°07′	850–1700		Oak-pine
Ostula	Aquila	18°30′	103°29′	550		Tropical
Parotas	Coalcomán			750–800		
Puerto Las Cruces	Coalcomán			1200–1450		Pine
Puerto Zarzamora				1200–1800		Oak-pine
Salitre	Coalcomán			1100–1800		Pine
San José	Aquila			750–1600		Pine & tropical
San Pedro	Aquila	18°15′	103°06′	450–600		Tropical
Sierra Naranjillo	Coalcomán			450–1550		Pine-oak
Sierra Torrecillas	Coalcomán			1400–2700		Pine-oak
Tizuapan (Tizupa)	Aquila	18°11′	103°02′	0–50		Tropical
Trojes	Coalcomán	18°57′	103°21′	400–500		Tropical
Villa Victoria	Villa Victoria			500–1600		Tropical & pine

			DISTRICT OF HUETAMO			
Huetamo	Huetamo	18°36′	100°54′		Awdr to Morelia	Tropical
San Lucas	San Lucas	18°34′	100°47′		Awdr to Huetamo	Tropical
Santa Cruz	San Lucas	18°25′	100°36′			Tropical
Tacupa	San Lucas			380		Tropical
Tario	San Lucas					Tropical
Tiquicheo	Tiquicheo	18°55′	100°45′	450–600	Awdr to Morelia	Tropical
			DISTRICT OF ZITACUARO			
Aguila (El Aguila)	Zitácuaro			2700–2800		Pine-oak
Ahorcados (Los Ahorcados)	Zitácuaro			2400		Pine-oak
Alumbres (Los Alumbres)	Zitácuaro			1250		
Angangueo	Angangueo	19°36′	100°18′	2100–2200	Paved highway to Zitácuaro	Pine
Aputzio	Zitácuaro			1950–2300		Oak
Benito Juárez (see Laureles)						
Bosque	Zitácuaro			1800	Awdr to Zitácuaro	Oak
Cacique	Zitácuaro			2350–3350		Pine-oak
Campana (La Campana)	Zitácuaro			2000–2300		Oak
Canoas (Las Canoas)	Zitácuaro			2600–2650		Oak-pine
Capulín	Estado de México	19°22′	100°18′			Oak
Cerro de los Magueyes	Zitácuaro					
Cerro Pelón (Pelón Hill)	Zitácuaro			2600–3600		Pine-oak
Coatepec	Zitácuaro			1950	Awdr to Zitácuaro	
Copándiro	Zitácuaro			1900–2600		Oak-pine
Coyota	Zitácuaro			1700–1900		
Dos Ríos	Zitácuaro	19°20′	100°28′	1800		
El Aguila (see Aguila)						
El Puerto (see Puerto)						
El Sauce (see Sauce)						
Enandio (Nandio, Salto de Enandio)	Zitácuaro			1500–1850		Oak

MICHOACAN

DISTRICT OF ZITACUARO

LOCALITY	MUNICIPALITY	APPROXIMATE COORDINATES LAT. N.	APPROXIMATE COORDINATES LONG. W.	ALTITUDE METERS	ACCESS ROADS	PREDOMINANT FOREST VEGETATION
Encarnación	Zitácuaro				Awdr to Zitácuaro	
Florida (La Florida)	Zitácuaro			1300–1600		Tropical
Galeras	Zitácuaro			2400–2500		
Guajes (Los Guajes)	Tuzantla			1000–1350		Tropical
Guanoro	Benito Juárez			1500–1900		Oak
Ipazote (Ypazote hill)	Zitácuaro			2150–2450		Oak-fir
Jungapeo	Jungapeo	19°28′	100°30′	1500–1850	Paved highway to Zitácuaro	Tropical
Jurungueo (Jurungeo)	Zitácuaro					
La Campana (see Campana)						
La Florida (see Florida)						
Las Canoas (see Canoas)						
Las Lomas (see Lomas)						
Las Pilas (see Pilas)						
Laureles (Benito Juárez)	Benito Juárez	19°18′	100°27′	1200–1700	Awdr to Zitácuaro	Oak
Loma Larga	Zitácuaro			1850–1950		Oak
Lomas (Las Lomas)	Zitácuaro			1900–1950		
Los Ahorcados (see Ahorcados)						
Los Alumbres (see Alumbres)						
Los Guajes (see Guajes)						
Los Macheros (see Macheros)						
Los Pinzanes (see Pinzanes)						
Los Tepehuajes (see Tepehuajes)						
Macheros (Los Macheros)	Zitácuaro			2300–2400		Oak
Macho de Agua	Zitácuaro			2300–2400		Oak-pine
Mango	Zitácuaro			2000–2100		
Manzanillos	Zitácuaro			2100–2200	Paved highway to Zitácuaro	

Nihuatlán	Donato Guerra, Estado de México?			2500–2550		Pine-oak
Ocurio	Zitácuaro			2000		
Pelón Hill (see Cerro Pelón)						
Piedra de Cal	Tuzantla			1300		Tropical
Pilas (Las Pilas)	Zitácuaro			2100		
Pinzanes (Los Pinzanes)				950–1300		Tropical
Puerto (El Puerto)				1450–1550		
Rincón						
Salitre	Tuzantla			675		Tropical
San Andrés (San Andrez)	Zitácuaro			2050–2150		
San Felipe	Zitácuaro			1900–2000		Oak
San José del Río	Zitácuaro			1900		
San José Purua	Jungapeo			1450–1950	Paved highway to Zitácuaro	Tropical
Santa Ana	Benito Juárez			1325		Tropical
Sauce (El Sauce)	Zitácuaro			1550–1900		
Seis Palos	Zitácuaro			2400		Pine
Sicate (see Zicate)						
Silva	Zitácuaro			2100–2400		Oak
Tepehuajes (Los Tepehuajes)	Tuzantla			600		Tropical
Tiamoro	Tuzantla			1300–1500		Tropical
Tiripitío (Tiripitillo)	Tuzantla			1000–1150		Tropical
Tuxpan	Tuxpan	19°35′	100°28′	2300		
Tuzantla	Tuzantla	19°12′	100°33′	700–800		Tropical
Ypasote hill (see Ipazote)						
Zicate (Sicate)	Benito Juárez			1900		Oak
Zirahuato	Zitácuaro			1900–2900		Oak
Zitácuaro	Zitácuaro	19°26′	100°22′	1600–2200	Paved highway to Mexico and Morelia	

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THE GENERA OF GERANIACEAE IN THE SOUTHEASTERN UNITED STATES [1]

KENNETH R. ROBERTSON

GERANIACEAE A. L. de Jussieu, Gen. Pl. 268. 1789, "Gerania," nom. cons.

(GERANIUM FAMILY)

Annual, biennial or perennial herbs [infrequently shrubs to trees; stems sometimes succulent] with simple and often glandular trichomes; underground stems, rhizomes [enlarged tubers and roots] frequently produced. Leaves opposite or alternate, palmately or pinnately lobed or compound [rarely simple and entire], palmately veined, stipulate, the petioles sometimes persistent. Inflorescences terminal or axillary, variable but basically cymose and sometimes condensed into umbels [rarely solitary], bracteate. Flowers perfect [or imperfect] and regular to slightly [or distinctly] irregular, 5-merous [rarely some parts fewer by abortion]. Sepals mostly distinct, persistent, imbricate. Petals distinct, often emarginate, imbricate, or convolute in aestivation [rarely absent]. Androecium obdiplostemonous [or of 5 bundles of three stamens], the stamens all fertile or some reduced to staminodia or scales; filaments connate at the base or distinct; anthers versatile, 2-locular at anthesis, opening lengthwise; nectar glands usually alternating with the petals. Gynoecium of 5 carpels united to an elongated columella, styles united to the columella, forming a beak on the ovary and fruit [or almost absent], 5-fid at the apex; stigmas distinct, ligulate to clavate [or filiform], ovary superior, 5-lobed, 5-loculate, the ovules 2 in each locule, anatropous to campylotropous, superposed and

[1] Prepared for a generic flora of the southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of the National Science Foundation (Grant GB–6459X, principal investigator, Carroll E. Wood, Jr.). This treatment follows the format established in the first paper in the series (Jour. Arnold Arb. **39:** 296–346. 1958). The area covered includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants in this area, with additional information from extraterritorial taxa in brackets. References I have not seen are marked by an asterisk.

I am most grateful to Dr. Carroll E. Wood, Jr., for his continuing advice and to Dr. Duncan M. Porter (Missouri Botanical Garden and Washington University) for carefully reviewing the manuscript. Mrs. Nancy Dunkly aided in typing the manuscript and checking the bibliography. A preliminary paper on the Geraniaceae written by Dr. Kenneth A. Wilson for the generic flora project has been consulted. Figures *a* and *c–m* were drawn by A. D. Clapman; figure *b* is the work of the late Dorothy H. Marsh. Dr. Wood collected most of the plant materials and prepared the dissections for the illustration. Dr. J. W. Thieret has kindly called attention to his finding of *Geranium texanum* in three parishes in Louisiana and has sent documenting specimens (deposited in A).

pendulous from axile placentae. Fruit a schizocarp, usually dehiscing elastically into 5 one-seeded mericarps that separate from the persistent columella with a part of the style forming an awn on the apex of the mericarp, the awn hygroscopic, becoming revolute or spiralled. Seeds without endosperm; embryo curved, with plicate to convolute incumbent cotyledons, often green. Embryo sac development of the Polygonum type, embryo development of the Asterad to Onagrad types. (Geranieae of Engler & Prantl, Knuth, and Scholz.) TYPE GENUS: *Geranium* L.

Five genera and about 700 species widely distributed in temperate and subtropical regions of both hemispheres; essentially restricted to high altitudes in the tropics. *Geranium* and *Erodium*, with both indigenous and naturalized species, represent the family in North America. A number of species of *Pelargonium* L'Hérit. ex Aiton, the horticultural "geraniums," a predominantly South African genus of about 250 species, are commonly cultivated in our area but are not naturalized although several are ephemeral escapes in California. *Sarcocaulon* (DC.) Sweet (six species) is South African, and *Monsonia* L. (about 30 species) occurs both north and south of the Sahara Desert in Africa and eastward to India.

These five genera comprise the Geranieae of Engler & Prantl, Knuth, and Scholz, and the Geraniaceae of Airy Shaw (in Willis), a very natural group with two ovules per carpel and the carpels in fruit separating into one-seeded mericarps, each with a curved or curled awn. The Biebersteiniaceae, Dirachmaceae, Ledocarpaceae, and Vivianiaceae, which differ in the number of ovules per carpel and in fruit structure, are often included in the Geraniaceae, but the taxonomic affinities of these families need further study. The Biebersteiniaceae have recently been placed with the Rosaceae (Bortenschlager), the Dirachmaceae in the Tiliales (Hutchinson), and questionably related to the Greyiaceae (Airy Shaw), the Ledocarpaceae in the Malpighiales (Hutchinson), and the Vivianiaceae in the Pittosporales (Hutchinson) or in the Centrospermae (Bortenschlager). There is rather general agreement that the Geraniaceae, sensu stricto, the Oxalidaceae, and the Tropaeolaceae belong together in a single order.

The schizocarp of the Geraniaceae is rather complex, and differing and inconsistently applied terminology has created confusion. At the base of the fruit are five mericarps (cocci, carpel bodies) which reflect the five lobes (locules) of the ovary. Arising immediately above is an elongated and more or less cylindrical rostrum (stylar column, beak), the apex of which abruptly tapers into the stylar beak, a narrow cylinder five-fid at the apex. Passing through the center of the fruit from the receptacle to the tip of the rostrum is a persistent columella (central column, stylar column, or rostrum), which has been said variously to be receptacular, ovarian, or stylar in origin. At maturity the fruits dehisce elastically or even explosively with the mericarps and awns separating from the columella. The awns, evidently strips of stylar material that before dehiscence form vertical bands on the rostrum, are hygroscopic and at dehiscence become revolute or spiralled, usually remaining attached to the mericarps

and either remaining affixed to the apex of the rostrum or not. The seeds are either ejected from the mericarps or retained within them.

Reported chromosome numbers are *Sarcocaulon Burmannii*, $2n = 44$; *Monsonia senegalensis*, $2n = 24$, *M. longipes*, $2n = 38$; *Pelargonium*, $2n = 9$ (haploid sporophyte), 14, 16, 18, 20, 22, 32, 36, 38, 44, 45, 54, 56, 60, 66, 72, 77, 81, 88, and 90, with 18 and 22 occurring most frequently; *Erodium*, $2n = 18$, 20, 27, 30, 36, 40, 48, 54 (56?), 60; and *Geranium*, $2n = 18$, 20, 22, 24, 26, 28, 32, 34, 36, 38, 42, 48, 50, 52, 56, 64, 68, 84, 128.

Pollen grains of the Geraniaceae are 3-colpate or 3-colporate with striate to reticulate exine sculpturing. Bortenschlager recognized seven distinct pollen types based on aperture type and sculpturing patterns. Most species of *Erodium* lack supratectate processes, while most of those of *Geranium* have mono- or dimorphic processes, although the pollen of certain species in both genera is indistinguishable. *Monsonia* and *Sarcocaulon* are palynologically identical, and *Pelargonium* has several distinct pollen types.

The studies of Konrad Sprengel, who first observed insect pollination scientifically and proposed the theory of cross-pollination, began with observations on *Geranium sylvaticum*. Since that time the pollination of numerous species of *Geranium*, *Erodium*, and *Pelargonium* has been investigated. The petals of most species are usually some light to dark shade of red to blue with the more intensely colored veins forming nectar guide lines that converge toward the center of the flower. Some species also have darker-colored spots toward the base of one or more petals, and in *Erodium* and *Pelargonium* there is a trend toward irregular corollas. A nectar-secreting spur of the uppermost sepal is adnate to the pedicel in *Pelargonium* species, and each of the five sepals of *Monsonia parvifolia* has a small spur. Species of the other genera have five nectar glands alternating with the petals. In some species the odor of the flower is evidently more important than corolla markings in the attraction of insects. Hymenoptera, and to a lesser degree, Lepidoptera, Diptera, and Coleoptera, are important pollinators; some large-flowered *Pelargonium* species of South Africa are visited by sun birds (Nectariniidae).

Numerous chemical substances have been identified in the Geraniaceae. Tannins have been reported in *Geranium*, *Pelargonium*, *Monsonia*, and *Erodium* and are especially abundant in the subterranean parts of perennial *Geranium* species. Gallic and ellagic acids are known from *Erodium cicutarium* and several species of *Geranium*, including *G. maculatum*, and catechins have been isolated from *G. pratense* and *G. palustre*. Essential oils occur in the glandular trichomes of a few *Geranium* species and in many *Pelargonium* species and hybrids. Most *Pelargonium* species accumulate tartaric acid, but those of *Geranium* and *Erodium* do not. The bark of xerophytic species of *Sarcocaulon* is rich in aromatic resins and waxes. The numerous species, hybrids, and cultivars of *Pelargonium*, the widely grown ornamental garden "geraniums," account for the principal economic importance of the family. In addition to the commonly cultivated pelargoniums, several species of *Geranium* and *Erodium* are grown for their

interesting appearance or showy flowers. Geranium oil used in perfumery, often as a substitute, extender, or adulterant for more expensive essences such as attar of roses, is extracted from several species of *Pelargonium*, particularly *P. graveolens* and *P. odoratissimum*. Extracts from various species of *Geranium* are used as astringents and aphrodisiacs and for tanning and dyeing, while extracts from *Monsonia ovata* and *Pelargonium antidysentericum* are used for the treatment of dysentery. *Erodium cicutarium* and some other species are important forage crops, but sometimes become rampant weeds.

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Key to the Genera of Geraniaceae in the Southeastern United States

General characters: *annual to perennial herbs with palmately or pinnately lobed to dissected, stipulate leaves; inflorescences terminal or appearing axillary, basically cymose, sometimes condensed into determinate umbels; flowers 5-merous, perfect, regular to slightly irregular, sepals mostly distinct, imbricate; petals distinct, imbricate or convolute; androecium obdiplostemonous, all stamens fertile or some reduced to staminodia or scales; gynoecium 5-carpellate with an elongated central columella, the ovary superior, ovules 2 per carpel, only one maturing; fruit a beaked schizocarp dehiscing into 5 mericarps with a strip of stylar tissue forming a hygroscopic awn on each; embryo curved, endosperm absent.*

Leaves palmately lobed; all stamens with anthers (except in *G. pusillum*); ultimate peduncles with 2 flowers; mericarps rounded at base. ejecting the seed; awn of mericarp revolute, glabrous or puberulent on the inner surface. ..... 1. *Geranium*.

Leaves pinnately lobed or dissected; only the inner 5 stamens with anthers; peduncles terminating in a several-flowered umbel; mericarps pointed at the base, retaining the seed; awn of mericarp spiraling, pubescent on the inner surface. ..... 2. *Erodium*.

1. **Geranium** Linnaeus, Sp. Pl. 2: 676. 1753; Gen. Pl. ed. 5. 306. 1754.

Annual to perennial herbs [rarely shrubs to small trees]; stems of two kinds, herbaceous and leafy flowering stems with ± swollen nodes, and thickened, condensed, often potentially perennial, basal stems or rhizomes underground or at ground level; roots branched or unbranched taproots or numerous adventitious roots originating from the condensed stems or rhizomes. Leaves mostly circular in outline, palmately lobed [infrequently dissected, entire or pinnate], the lobes variously toothed or incised; basal leaves long-petiolate, the petioles often ± persistent; cauline leaves opposite or alternate (especially in the inflorescence), ± similar to basal leaves but usually smaller and with shorter petioles. Inflorescences basically cymose, the ultimate peduncles [1]2-flowered and [2]4-bracteate, usually terminal but by continued and sympodial branching within the inflorescences often appearing axillary. Flowers perfect [rarely imperfect], regular. Sepals 5, with obtuse to caudate apices. Petals 5, pubescent at least basally, frequently emarginate at apex, white to some shade of pink or red-purple [blue to blackish-purple], the veins more intensely colored, reticulately veined throughout or only apically. Stamens 10, in two

FIGURE 1. **Geranium.** a–j, *G. maculatum*: a, flowering plant showing erect annual shoot and perennial underground rhizome, × ¼; b, flower at anthesis — note inner whorl of dehiscing stamens and still closed stigmas, × 1½; c, stamen of outer whorl, × 4; d, gynoecium with nectar glands on receptacle below pubescent ovary, sepals, petals, and stamens removed (petal attachment points triangular, stamen attachment points open circles), × 4; e, semidiagrammatic vertical section of same to show placentation, × 6; f, diagrammatic cross section of ovary with two superposed ovules in each locule, × 8; g, dehisced fruit showing mericarps attached to recurved hygroscopic awns, × 2; h, seed, × 5; i, embryo, × 5; j, cross section of embryo to show folding of cotyledons, × 5. k–m, *G. carolinianum*: k, tip of flowering and fruiting branch showing one sympodially branched inflorescence, × ½; l, flower with receptive stigmas, anthers mostly fallen, × 3; m, mature fruit before dehiscence (one sepal recurved) — note persistent filaments and connivent stigmas, × 2.

whorls, the outer whorl opposite the petals and maturing after the inner antesepalous whorl; filaments often of two lengths, basally connate, all bearing anthers (except in *G. pusillum*); nectar glands 5, alternating with petals, occuring on receptacular area between sepals and the inner whorl of stamens. Ovary frequently pubescent. Schizocarp elastically or explosively septicidal from base upwards, awns usually remaining attached to top of columella; mericarps rounded at base, each with a persistent awn, these glabrous or puberulent on the adaxial surface, recurving abaxially. Seeds mostly ejected from mericarps, the seed coat reticulate to smooth. Cotyledons long petiolate, transversely elliptic and somewhat asymmetrical when expanded, emarginate at apex and cordate at base, entire or slightly 3-lobed. (Including *Robertiella* Hanks in Hanks & Small.) LECTOTYPE SPECIES: *Geranium sylvaticum* L.; see L. T. Hanks & J. K. Small, N. Am. Fl. **25**: 4. 1907. (Name from Greek *geranion*, a crane, in allusion to the beaklike fruit; used by Dioscorides, see Gunther.) — CRANE'S-BILL, WILD GERANIUM.

A genus of 250–300 species widely distributed in temperate, montane, and subpolar regions of both hemispheres, extending into the tropics only in the mountains. Some species have amphiatlantic or subantarctic distributions. Major centers of diversification are the mountains of Europe, the Mediterranean region, the Cordilleras of South, Central, and western North America, and Hawaii. About 20 species are native and 12 naturalized in the continental United States; six of these (including four introduced) occur in our area.

The genus was divided by Knuth into 30 often unnatural sections based on longevity, habit, floral size, distribution, and the morphology of the rhizome, leaf, and inflorescence. Subsequent authors have rearranged the species into "series" or "groups" (Moore, Davis), have rejected Knuth's system without attempting a formal division of the genus (most authors of floras), or have accepted provisionally Knuth's sectional names, while admitting the inadequacy of his system (Carolin).

The only perennial species of *Geranium* in our area, *G. maculatum* L., is of common occurrence in diverse plant communities, especially of the eastern deciduous forests, but also in fields, meadows, forest openings, thickets, along stream banks, and along the edges of cleared land, from Maine and southern Ontario to southeastern Manitoba, northeastern South Dakota and north-central Nebraska, south to central Georgia and eastern Oklahoma. The occasional white-flowered individuals are sometimes separated from the typical rose-purple-flowered plants as forma *albiflorum* (Raf.) House. Placed by Knuth in his sect. *Sylvatica* (= sect. GERANIUM), *G. maculatum* with simple or branched horizontal rhizomes, was closely allied by Jones & Jones to three other species with unbranched, more or less vertical or oblique rhizomes: *G. pratense* L., $2n = 28$ (Eurasia, occasionally adventive in the northeastern United States), *G. erianthum* DC., $2n = 28, 30$ (northern Japan to Alaska and British Columbia), and *G. oreganum* T. J. Howell (northwestern United States). This group is

characterized by large flowers, only basally pubescent petals, short stigmas, and erect fruiting pedicels (sometimes recurved in *G. pratense*).

The six remaining species in our area have been placed in sect. COLUMBINA Koch (mostly small-flowered annuals with fine roots, leaves round to almost reniform in outline, calyx open or scarcely adpressed to the mature fruit). Carolin, in his treatment of the Malesian species, states that species grouped around *Geranium carolinianum* in North America have some links with "a complex group — containing Knuth's sections *Chilensia*, *Australiensia*, and fragments of *Striata* and *Columbinum* — extending from India, through Malesia, temperate Australia, New Zealand, and the Subantarctic islands, to southern America, ..."

Geranium carolinianum L. (including *G. Langloisii* Greene), $2n = 52$, is indigenous throughout temperate North America, mostly in dry disturbed habitats. Distinguished from other species in the area by its awned sepals, pedicels less than twice as long as the sepals, and mature carpels hirsute with long antrorse trichomes, plants of this species are quite variable, particularly in density of pubescence and structure of the inflorescence. Plants with the upper internodes greatly shortened and the flowers in compact. many-flowered, determinate umbels are sometimes separated as var. *confertiflorum* Fernald, confined mostly to the northeastern United States but occurring also in the mountains of North Carolina. Until recently known only from south and central Texas, *G. texanum* (Trelease) Heller, with circular-ovate sepals and an eglandular rostrum, has recently been collected in Louisiana by J. W. Thieret. *Geranium Bicknellii* (including *G. longipes* Goodding non DC., *G. nemorale* Suksdorf; trans-Canada and northeastern United States), and *G. sphaerospermum* Fernald (questionably distinct from *G. carolinianum*; northern states and adjacent Canada) are closely related to *G. carolinianum*.

Possibly native in the western United States, but more likely an early introduction from Europe, *Geranium dissectum* L. (including *G. laxum* Hanks in Hanks & Small), $2n = 22$, is locally naturalized and abundant in disturbed habitats in the eastern United States from Massachusetts to Michigan south to Georgia and Texas. It is distinguished from the very similar *G. carolinianum* by the pubescent but not long hirsute mericarps and more strongly reticulate seeds.

Three introduced European species of this section are found locally in disturbed habitats in the eastern United States. *Geranium columbinum* L., $2n = 18$ (indumentum eglandular, pedicels twice as long as the awned sepals, mericarps glabrous) occurs from New York west to the Dakotas and south to North Carolina and Georgia; it is also reported from one county in Washington and along the Columbia River in Oregon. Widespread in the Pacific Northwest, *G. pusillum* L., $2n = 26$ (sepals acute, several filaments without anthers, fruit rostrum very short, mericarps pubescent) is infrequent eastward to Massachusetts and south to North Carolina. Oklahoma, and Utah. *Geranium molle* L., $2n = 26$ (sepals acute, all stamens fertile, fruit rostrum short, mericarps obliquely wrinkled — or smooth in forma *Preuschoffii* Abromeit), ranges from Newfoundland

to British Columbia and the Pacific States and south to North Carolina, Tennessee, and Illinois.

Geranium Robertianum L., Herb Robert, $2n = 64$ (32, 54?, 56), of sect. ROBERTIANA Boiss., the only species of the genus in North America with completely palmately compound leaves with the middle segment prominently petiolulate, occurs to the north of our area, extending as far south and west as Virginia, West Virginia, Ohio, Indiana, Illinois, and Nebraska. Amphiatlantic in distribution, this species is common throughout Europe, and it has been introduced into many regions of the world, including the Pacific United States.

The prevalent somatic chromosome number, especially in the perennial species. is 28. There are evidently two chromosomal races of *Geranium phaeum* L., $2n = 14$ and 28. A polyploid series based on 14 exists, with reports of $2n = 42$ (2 species), 56 (numerous species), and 84 (*G. sanguineum* L.). Other base numbers are found, particularly in the annual species, the most frequent being $2n = 26$ and 52; aneuploidy and polyploidy are fairly common. *Geranium Robertianum* has been reported as $2n = 32$, 56 (54?), 64, with the last the most frequent; further studies are needed to determine the scope of chromosomal variation in this species. The closely related *G. purpureum* Vill. is consistently $2n = 32$. *Geranium anemonifolium* L'Hérit. ex Aiton, a species from Madeira and the Canary Islands allied to *G. Robertianum*, evidently has two races, $2n = 68$ and 128 (the highest number known in the genus).

Hybridization between *Geranium* species is infrequent, occurring mostly between closely related species. Documented hybrids involving species indigenous to North America are thus far unknown, but the species in the western United States have not been closely examined in this respect. Naturally occurring hybrids have been found between two European species of sect. COLUMBINA with different base chromosome numbers, *G. bohemicum* L., $2n = 28$, and *G. lanuginosum* Lamarck, $2n = 48$, the hybrid chromosome number being $2n = 38$. The seeds of these two species do not readily germinate without exposure to heat and plants often appear in areas after forest fires.

The pollen of *Geranium* species is 3-colporate with round to lolongate ora and short colpi. The exine is semitectate with the infrategillar bacula circular in cross section. More or less uniform suprategillar structures are found in the majority of species, with strongly dimorphic processes occurring in many circum-Pacific species, including *G. Richardsonii* of the western United States, and *G. Hernandezii* of Mexico. The pollen of a few species lacks suprategillar processes and has a striate-reticulate exine like most species of *Erodium*.

Numerous large-flowered species of *Geranium*, such as *G. maculatum*, *G. palustre*, and *G. pratense*, are strongly proterandrous and mostly cross-pollinated. As the flowers open, the outer whorl of stamens curves out and downward while the inner whorl remains erect, the anthers soon dehiscing (see FIGURE 1b). The outer whorl then becomes erect, the anthers dehisce, and the filaments again recurve, as do those of the inner

whorl. After this the anthers frequently become detached from the filaments, and the lobes of the style open, exposing the stigmatic surfaces. In the smaller-flowered species, such as *G. carolinianum*, that attract few insects, there is a tendency for homogamy with increased probability for self-pollination. Some species of *Geranium* and *Erodium* have both perfect flowers and smaller and functionally carpellate ones that are usually gynodioecious in distribution. (Gynomonoecism, androdioecism, andromonoecism, and true dioecism are rare in the Geraniaceae.)

There have been several detailed studies of intraspecific variation in European *Geranium* species. *Geranium Robertianum* and the closely related *G. purpureum* (sometimes treated as a subspecies of the former) were studied genecologically by Böcher and by Baker. Böcher & Lewis investigated variations in leaf and petal morphology, height, habit, time and length of the flowering period, longevity, pubescence, and flower color in 36 strains of *G. sanguineum* from nine European countries. The polymorphic breeding system of *G. sylvaticum* has been investigated numerous times, most recently by Putrament (1962) and Vaarama & Jääskeläinen (1967). Except for Martin's study of *G. maculatum* and Russell's brief account of *G. Richardsonii*, detailed studies of variability in North American species are lacking but would probably be quite informative.

Most species of *Geranium*, including all in North America, have two types of stems. The above-ground floriferous and annual stems are the more prominent. This kind of stem and the basal leaves arise from a thickened and condensed basal stem (caulorrhiza, caudex) which is usually at or below ground level, and may be horizontal and forming a rhizome, oblique, or vertical. In many species this basal stem is the perennating organ, but some form of basal stem is present even in annual species. A taproot and/or numerous adventitious roots arise from the basal stem.

In some species the schizocarp dehisces explosively with such force that the seeds are thrown out of the mericarps and travel laterally for several hundred centimeters. Observations made by C. E. Wood, Jr. (personal communication), on *Geranium maculatum* indicate that when undisturbed the fruit opens over a short period with the mericarps separating from the columella and the adaxial side, where the dehiscence suture is located, becoming oriented away from the axis due to the revoluting awns. At this point the seeds are forcibly ejected from the mericarps due to the drying and subsequent contraction of the carpel wall. The awns become even more revolute after dehiscence (see FIGURE 1g). Martin, in her study of this species found that the fruits would dehisce explosively if subjected to a slight mechanical stimulation; this violent dehiscence evidently occurs spontaneously in nature with the awns and/or mericarps becoming detached from the fruit.

Some species of *Geranium* are commonly grown as ornamentals. The most frequently encountered species in eastern North America are *G. sanguineum* L., $2n = 84$, which has several varieties and named cultivars, and *G. grandiflorum* Edgew.

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2. Erodium L'Héritier ex Aiton, Hortus Kew. 2: 414. 1789.

Annual or biennial herbs [sometimes perennial, caespitose or shrubby], at first acaulescent rosette plants, later with several ± jointed elongate, simple or branched stems often arising and radiating from generally unbranched taproots. Leaves longer than broad, pinnately compound [or lobed; rarely simple or palmate], the leaflets toothed, lobed or subdivided,

sessile or shortly petiolulate; basal and cauline leaves similar, the latter opposite [or all alternate] and tending to be more strongly lobed, divided, or subdivided. Inflorescences determinate umbels, arising from the rosette and/or from nodes of elongated stems; ultimate peduncles several flowered [infrequently with 1 or 2 flowers]. Flowers perfect [rarely imperfect. the plants dioecious], regular to slightly irregular. Sepals 5, often mucronate or aristate. Petals 5, glabrous, equal or the two upper smaller [rarely absent], pink to violet, purple [white, blue or lilac, very rarely yellow or deep red], the veins typically more intensely colored, sometimes with a dark or blackish spot near the base of the two upper [or all] petals. Fertile stamens 5, the outer antepetalous whorl reduced to staminodia [or scales]; filament bases sometimes with two lateral teeth. Ovary pubescent. Schizocarp dehiscing mostly from apex downwards, the mericarps and awns becoming completely detached from the columella; mericarps tapering toward base; awns persistent on mericarps [or deciduous], pubescent on adaxial surface, lower portion spirally coiling when freed from columella. Seed smooth, retained within mericarp. LECTOTYPE SPECIES: *E. crassifolium* L'Hérit. ex Aiton = *E. hirtum* (Forsk.) Willd. non Jacq.; see L. T. HANKS & J. K. SMALL, N. Am. Fl. 25: 21. 1907. (Name from Greek *erodios*, heron, in comparison of the shape of the fruit to a heron's bill.) — HERON'S-BILL, STORK'S-BILL, ALFILERIA, FILAREE, PIN-CLOVER.

A genus of 60 to 80 species centered in Mediterranean Europe, North Africa, and the Middle East; species have been introduced into most temperate regions of the world. Two sections are usually recognized, ERODIUM (§ *Plumosa* Boissier) (mericarp awns quickly deciduous and plumose on the adaxial surfaces with long silvery or yellowish trichomes) and BARBADA Boissier (awns persistent on mericarps, trichomes on adaxial surfaces short, adpressed, and reddish). The latter section was subdivided by Knuth into ten subsections based on leaf morphology, habit, rostrum length, petal size and shape, and density of indumentum.

In the United States at least ten species, all belonging to sect. BARBATA, have been reported, several being ephemeral escapes. Two introduced species, *Erodium cicutarium* (L.) L'Hérit. ex Aiton and *E. moschatum* (L.) L'Hérit. ex Aiton, both belonging to subsect. CICUTARIA, a taxonomically difficult group centered in the southwestern Mediterranean region, occur in our area. Both are also naturalized in the West, as are *E. Botrys* Bertol., $2n = 40$ (southern Europe and the Mediterranean region) and *E. brachycarpum* (Godr.) Thell. (including *E. obtusiplicatum* (Maire, Weiller & Wilczek) J. T. Howell and *E. Botrys* f. *montanum* Brumh.; North Africa), $2n = 40$. Apparently the western *E. macrophyllum* Hooker & Arnott (*E. californicum* Greene; related to *E. malacoides* (L.) L'Hérit. ex Aiton of southern Europe) and *E. texanum* Gray, $2n = 20$, placed by Knuth in subsect. GUTTATA, otherwise Mediterranean in distribution, are indigenous.

Erodium cicutarium, characterized by its eglandular apical mericarp pits, aristate sepals, sessile leaflets divided more than half-way to the midrib, and toothless anther-bearing filaments, is found in fields, roadsides, and waste places throughout most of the United States. It probably occurs sporadically in all states in our range but is poorly represented in herbaria. A very plastic species, particularly in habit, size, leaf shape, indumentum, and fruit morphology, *E. cicutarium* has had a tortuous nomenclatural history with numerous segregate species, subspecies, and varieties described and several classification schemes proposed (see Litardière in Briquet, Andreas, Rottgardt, Larsen, Tutin *et al.*, and Guittonneau). In Europe there are several chromosomal races with the predominant number being $2n = 40$, but $2n = 20$ is common and $2n = 36$, 48 and 54(56?) also occur; hexaploid populations, $2n = 60$, have been segregated as *E. danicum* K. Larsen. At least three morphological entities occur in Europe: a mostly tetraploid "field" type, a tetraploid "dune" type, and a mostly diploid "dune" type. The plants in the United States evidently correspond to the "field" type, *E. cicutarium* subsp. *cicutarium*, and the only chromosome number reported from this country is $2n = 40$. This species is also naturalized in Australia, Java, East Africa, and probably in most other temperate regions of the world.

Erodium moschatum, $2n = 20$, characterized by its glandular apical mericarp pits, acute to mucronate sepals, shortly petiolate leaflets divided less than half-way to the midrib, and anther-bearing filaments with two lateral teeth, is common in California and has been reported as an infrequent adventive in waste places and roadsides in northern Florida and the northeastern United States. It is also naturalized in East and South Africa and Australia.

The awn of the mericarp is pubescent inside and has a dextrorsely spiraled coiled portion, the spirillum, and an arching terminal portion, the flagellum. The awns are hygroscopic, the spirals loosening when moist and becoming tighter when dried. In nature, varying weather conditions cause the awns to coil and uncoil repeatedly, and this action evidently forces the seeds into the soil. The awns have been used to make hygrometers. The seed is usually retained within the tapering mericarps. At the apex of the mericarp are two flattened areas referred to as pits (foveae, foveoles) which are subdivided in some species by one or more ridges, giving the impression of furrows below the pits.

The base chromosome number in the genus is $x = 10$, with $2n = 20$ the most frequently reported number. Tetraploids are common, hexaploids have been recorded in three subsections, and one octoploid is known. Aneuploidy occurs in *E. cicutarium* (see above) and all reports for species in subsect. Absinthioidea are $2n = 18$. Most, if not all, species in this latter subsection are dioecious (see Davis & Roberts; illustration in Stefani, *et al.*).

The pollen of *Erodium* species is 3-colporate and most species lack suprategillar processes with the exine striate-reticulate. Three subtypes based on sculpturing patterns were distinguished by Bortenschlager. A

few species, including *E. texanum*, have strongly dimorphic suprategillar processes, like the pollen found in most *Geranium* species.

In the Southwest several species, particularly *E. cicutarium*, are important spring and winter range forage plants for domestic and game animals. Some species are also grown as ornamentals in rock gardens. *Erodium cicutarium* can be an aggressive weed, competing vigorously with crops such as alfalfa.

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ON THE ORIGIN OF THE ORCHIDACEAE, II [1]

LESLIE A. GARAY

The myriad things in nature are completely similar and completely dissimilar. This should be described as a great similarity in dissimilarity. — HUI SHIH (4th Century B.C.)

IN 1960, in discussing my ideas on the origin of the present-day complexity of the orchid family, I called attention to the presence of five distinct phyletic lines based on the disparity in their respective endomorphic and exomorphic features, as well as on the absolute genetic incompatibility among the members of each line with respect to the others. These kladogenetic lines which have evolved in a parallel manner represent distinct subfamilies known as APOSTASIOIDEAE, CYPRIPEDIOIDEAE, ORCHIDOIDEAE and NEOTTIOIDEAE. The plants referable to these subfamilies are all terrestrial. The epiphytic mode of life evolved through a secondary differentiation which occurred in the NEOTTIOIDEAE, giving rise to a fifth line or subfamily, the EPIDENDROIDEAE (4, 5).

This new departure from the commonly accepted classification into two main divisions — MONANDRAE and DIANDRAE, one *versus* two fertile anthers — has stimulated responses for the continuation of the old *status quo*. The fundamental difference between my thesis and those of my critics is the recognition of the evolutionary lines as natural systematic units, whereas in the opposing approaches, where the phyletic lines are randomly accommodated in some arbitrary categories, the taste and flavor of the ancient numerical system of Linnaeus is still cloyingly prevalent. A summary of the main approaches is given in FIGURE 1.

CRITIQUES AND CRITICAL POINTS

Apostasioideae. An attempt has been made by Vermeulen (13, 14) along the lines which were suggested in the past by Schlechter, Ridley, Takhtajan (12), and more recently by Hutchinson (8) to reinstate the APOSTASIOIDEAE to family status. Yet Stebbins and Khush (11) have convincingly shown that the stomatal complex in the APOSTASIOIDEAE is anomocytic, i.e., two guard cells without subsidiary cells, which is characteristic of the Orchidales. The Haemodorales or Liliales to which Apostasiaceae has been referred by several is characterized by a paracytic stomatal complex, i.e., two guard cells plus two subsidiary cells. This latter group seems to have arisen only once in evolutionary history of the monocotyledons.

[1] On the origin of the Orchidaceae [I]. Bot. Mus. Leafl. Harvard Univ. **19**: 57–96. 1960.

AUTHOR	MAIN DIVISIONS OF SYSTEM							
LINDLEY		CYPRIPEDEAE	OPHRYDEAE	ARETHUSEAE	NEOTTEAE	MALAXIDEAE	EPIDENDREAE	VANDEAE
BENTHAM	CYPRIPEDIEAE		OPHRYDEAE	NEOTTIEAE		EPIDENDREAE		VANDEAE
REICHENBACH	CYPRIPEDIEAE		OPHRYDEAE	OPERCULATAE				
				NEOTTIEAE		*EUOPERCULATAE*		
PFITZER	PLEONANDRAE		MONANDRAE					
			BASITONAE	*ACROTONAE*				
				Acranthae - Convolutae		*Acranthae* { *Duplicatae - Articulatae* } *Pleuranthae - Sympodiales Monopodiales*		
ROLFE	DIANDRAE		MONANDRAE					
			OPHRYDEAE	*NEOTTIEAE*		*EPIDENDREAE*		*VANDEAE*
SCHLECHTER		DIANDRAE	MONANDRAE					
			BASITONAE	*ACROTONAE*				
				Polychondreae		*Kerosphaereae*		
MANSFELD	DIANDRAE		THRAUOSPHAEREAE			KEROSPHAEREAE		
			OPHRYDEAE	*NEOTTIEAE*		*EPIDENDREAE*		*VANDEAE*
HATCH		CYPRIPEDIOIDEAE	ORCHIOIDEAE					
			BASITONEAE	*ACROTONEAE*				
DRESSLER AND DODSON	CYPRIPEDIOIDEAE		ORCHIDOIDEAE					
			ORCHIDEAE	*NEOTTIEAE*		*EPIDENDREAE*		
GARAY	APOSTASIOIDEAE	CYPRIPEDIOIDEAE	ORCHIDOIDEAE	NEOTTIOIDEAE		EPIDENDROIDEAE		
						EPIDENDREAE		*VANDEAE*
			ORCHIDEAE	*EPIDOGONEAE*		*Phaiinae*		*Cyrtopodiinae*
			DISEAE	*NEOTTIEAE*		*Dendrobiinae*		*Zygopetaliinae*
			DISPERIDEAE	*CRANICHIDEAE*		*Epidendriinae*		*Oncidiinae*
						Pleurothallidinae		*Vandiinae*

EWS

FIGURE 1. Summary of various systems of classification of ORCHIDACEAE.

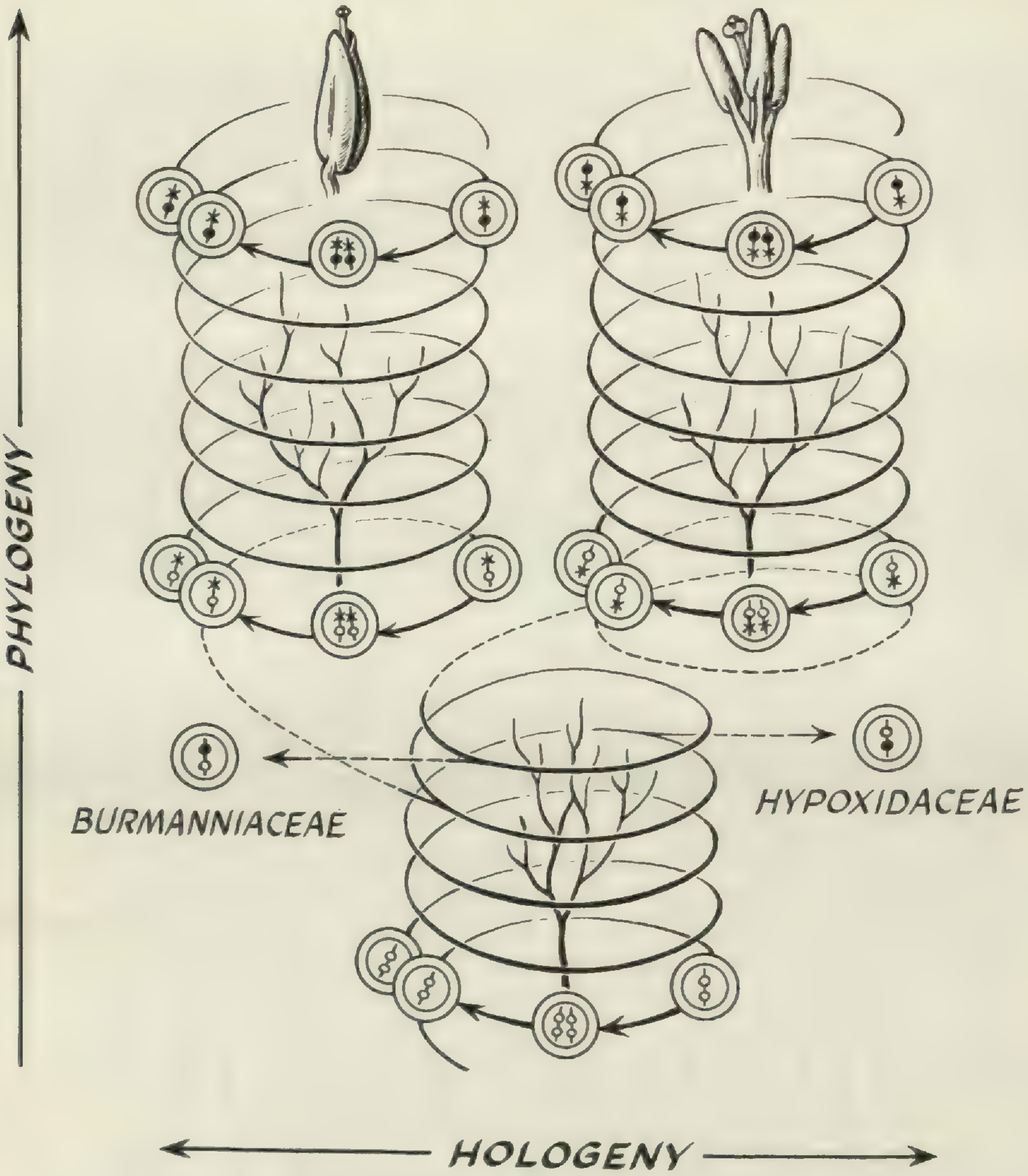

FIGURE 2. Phylogeny and hologeny of subfamily APOSTASIOIDEAE.

On the other hand Dressler and Dodson (3), Melchior (9), and De Vogel (2) in following Pfitzer consider the APOSTASIOIDEAE merely a tribe under the CYPRIPEDIOIDEAE, notwithstanding the absence of the vaguest superficial resemblance between members of these two subfamilies. As a matter of fact, the two genera that comprise the entire subfamily, *Apostasia* and *Neuwiedia*, are not even closely related to one another but are only relic survivors of ancient anagenetic lines. Their hologeny is depicted in FIGURE 2 (5). In many ways they resemble the remnants of a grand dinner from which it is no longer possible to reconstruct the complete menu.

Cypripedioideae. This taxon, like the APOSTASIOIDEAE, is a relic group (5, 12). It is composed of four superficially similar genera: *Cypripedium*, *Paphiopedilum*, *Phragmipedium*, and *Selenipedium*. The generic differentiation must have taken place in the obscure evolutionary past, perhaps shortly after the group as a whole was initiated, because of the absolute incompatibility among the members of each line with respect to the other lines. Lack of incompatibility among members of different genera is the rule rather than the exception in the ORCHIDOIDEAE, NEOTTIOIDEAE and EPIDENDROIDEAE (6).

The CYPRIPEDIOIDEAE has been accepted generally as a distinct subfamily, although its circumscription varies according to the interpreter. Recently Vermeulen, following in the footsteps of Lindley and Mansfeld, but not necessarily following their reasoning, proposed to elevate this group to family status, thus recognizing the Apostasiaceae, Cypripediaceae and Orchidaceae within the order Orchidales (13, 14). Indeed it makes no difference whether or not we recognize five subfamilies or five distinct families so long as the principles that must govern such steps do not become subservient to arbitrary decisions. Such a guide line, however, is wanting in Vermeulen's presentation.

Orchidoideae. In advancing the thesis that the APOSTASIOIDEAE and CYPRIPEDIOIDEAE must be regarded as distinct families, Vermeulen failed to recognize or appreciate the uniqueness of the ORCHIDOIDEAE, for he included it together with a newly proposed subfamily (although with an old and already known name, EPIDENDROIDEAE) in his new concept of the orchid family (13, 14). It is not difficult to recognize the reason for such an action, for the subfamily ORCHIDOIDEAE includes the genus *Orchis*, the nomenclatorial type of the Orchidaceae. Should one grant family status to each of the five subfamilies, the Orchidaceae will become one of the least significant families in the whole complex, with most of its members showing the strain of ancient isolation and overspecialization (6). The overwhelming majority of the species is in the subfamily EPIDENDROIDEAE. Thus, the interpretation of evolutionary phenomena which led to the idea of the fragmentation of the Orchidaceae into several families has suddenly given way to a completely unrelated aspect of scientific endeavor: nomenclatorial priorities.

The subfamily ORCHIDOIDEAE is composed of well-advanced species, so far without any trace or evidence documenting its origin and progressive differentiation from a lesser evolved stock. The highly evolved pollinia with pollen grains solidly united into massulae which are borne on caudicles with hygrometric behavior (4, 6), the complete basitonic fusion between the anther and the column (4), and the occurrence of polystely in the roots and tubers (15) are all strictly limited to this subfamily.

The column in the ORCHIDOIDEAE is very dissimilar to that found in other subfamilies; the only fertile anther is formed in such a way that it is completely adnate to, and embedded in, the columnar tissue. To derive the column of the NEOTTIOIDEAE and EPIDENDROIDEAE from the ORCHI-

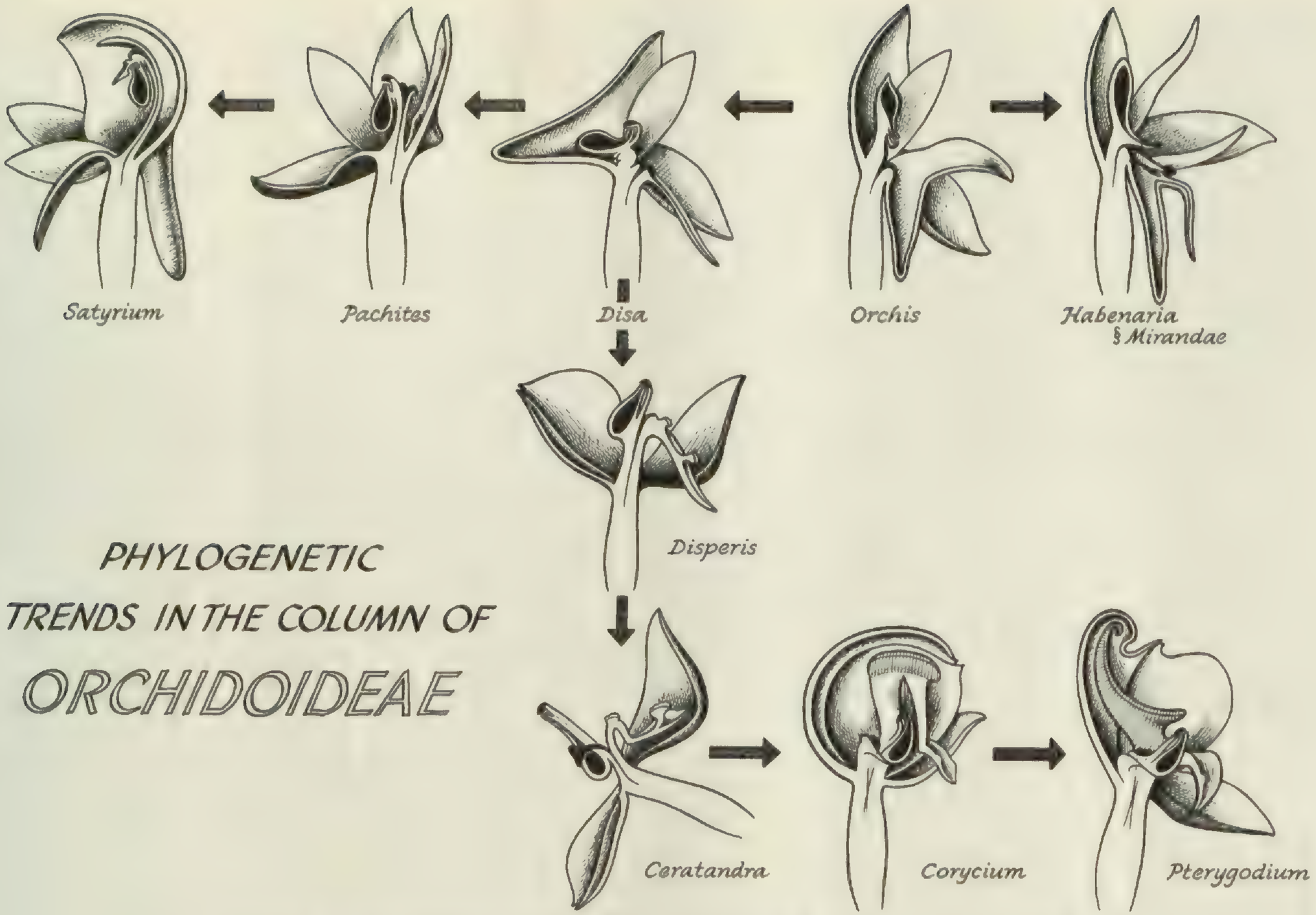

FIGURE 3. Phylogenetic trends in the column of subfamily ORCHIDOIDEAE.

DOIDEAE or *vice versa*, would require the impossible reversal of the true morphological apex of the anther. Although such a reversal may seemingly come about through inclination of the anther, such a directional movement merely changes the position of the true apex without reversing it, as shown in FIGURE 3 depicting that phylogenetic trend (6). It is evident that the various stages in the gyration of the column are intimately correlated with the entomophilous nature of the flowers, each step progressively leading toward irreversible overspecialization, and hence to ultimate extinction.

Neottioideae. This kladogenetic line is the most successful one, as well as the most important one in the whole family, for it provides all of the evidence necessary for the interpretation of the various evolutionary pathways that make the present-day complexity understandable. It was within the framework of this subfamily that evolutionary developments (or rather evolutionary innovations) leading to a secondary kladogenetic differentiation, EPIDENDROIDEAE, and opening all avenues toward a successful expansion in both structural diversity and spatial distribution, occurred.

The column in the NEOTTIOIDEAE and in the EPIDENDROIDEAE is strikingly dissimilar to those of the other subfamilies, although all share in common a certain degree of fusion between the style and the filament or filaments. Such a fusion must have occurred independently many times during the early history of the family, but only four kladogenetic lines have been carried through to the present. The single fertile anther is free and movably connected with the column at its acrotonic end.

A closer inspection of the hologeny of this subfamily, FIGURE 4 (5), seems to focus on the presence of two major anagenetic trends. One of these is expressed in the aggregation of free pollen grains into tetrads and the tetrads into pollinia, while the other can be traced in the progressive modification of one of the stigmatic lobes into a new organ called the rostellum. Although the interaction of these two trends seems to provide an inexhaustible reservoir for diversity, the true expansion of the orchid family owes its existence to the coaction of a third evolutionary innovation, the development of the epiphytic mode of life. The main anagenetic lines are designated here as tribe Cranichideae, tribe Neottieae, and tribe Epipogoneae.

Epidendroideae. The members of this subfamily are all advanced types. In regard to the development of floral parts, the EPIDENDROIDEAE represents the final stage in the organogenesis of the column, because there is a complete fusion of the reproductive organs in every species. Correlated with this fusion is a fully functional rostellum to which the pollinia are attached. There is also a further correlation between the position of the anther and the rostellum and between the position of the rostellum and structural changes in the pollinia (6). An inspection of longitudinal sections of developing flower buds, which are assembled according to their affinities in FIGURES 5 and 6, clearly shows that the

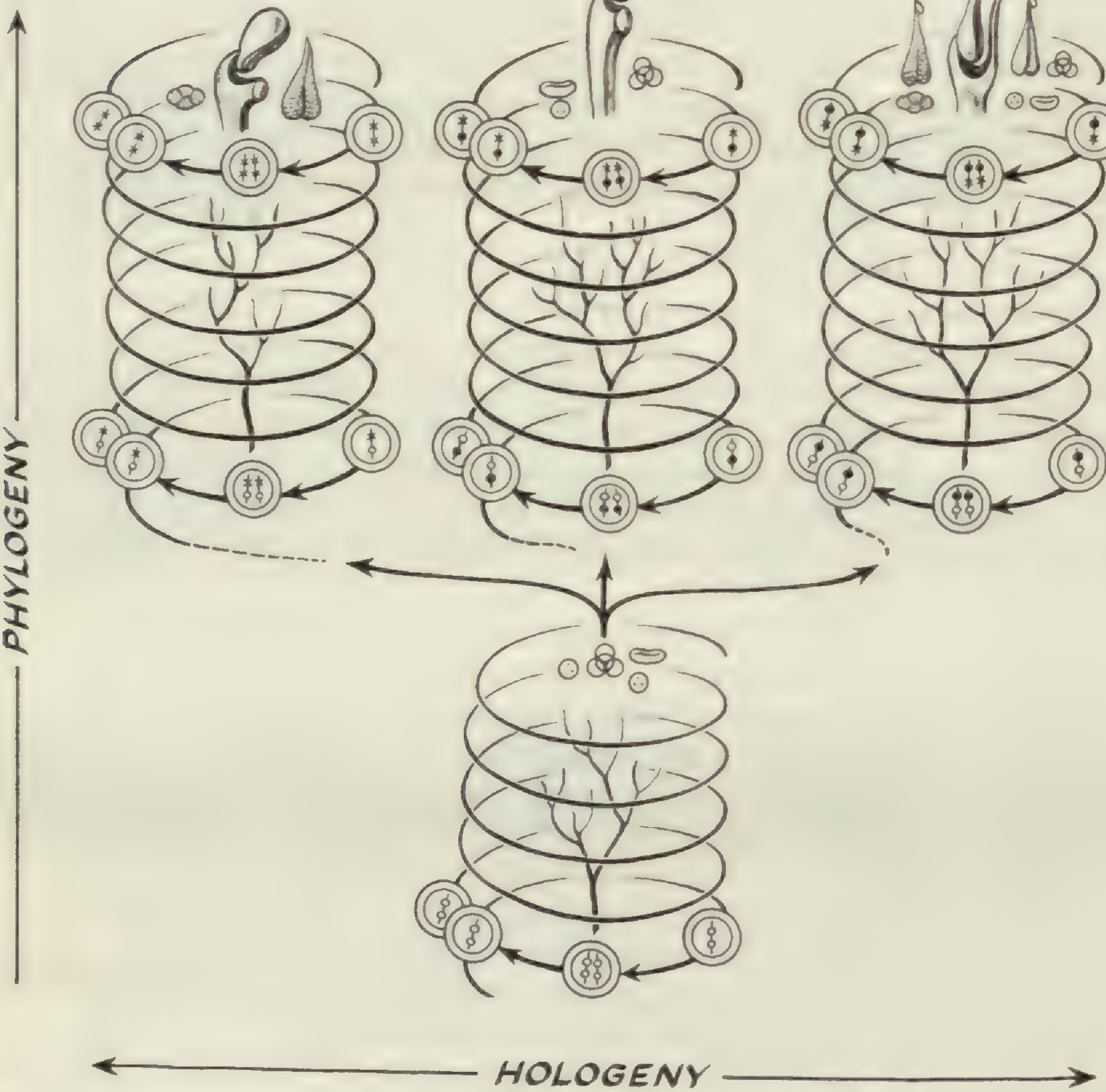

FIGURE 4. Phylogeny and hologeny of subfamily NEOTTIOIDEAE.

various floral types fall within two anagenetic lines or natural evolutionary units: 1, column with an erect anther and an ascending (arrect) rostellum to which the pollinia are attached without appendages, and 2, column with an incumbent anther and a horizontally projecting (porrect) rostellum to which the pollinia are affixed through well-developed stipes. These two evolutionary lines are designated here as tribe Epidendreae and tribe Vandeae respectively (6).

The columnar structure in the Epidendreae is very similar to that of the Cranichideae of the subfamily NEOTTIOIDEAE. Anagenetic differentiation in the NEOTTIOIDEAE is expressed in three distinct lines or natural evolutionary units (5). Because of the identity of the angle of the insertion of the anther and also of the ascending rostellum in both the Cranichideae and Epidendreae, I believe that the subfamily EPIDENDROIDEAE owes its existence to a secondary kladogenetic differentiation that took

FIGURE 5. Diagrammatic median longitudinal sections of column in developing buds of members of tribe EPIDENDREAE.

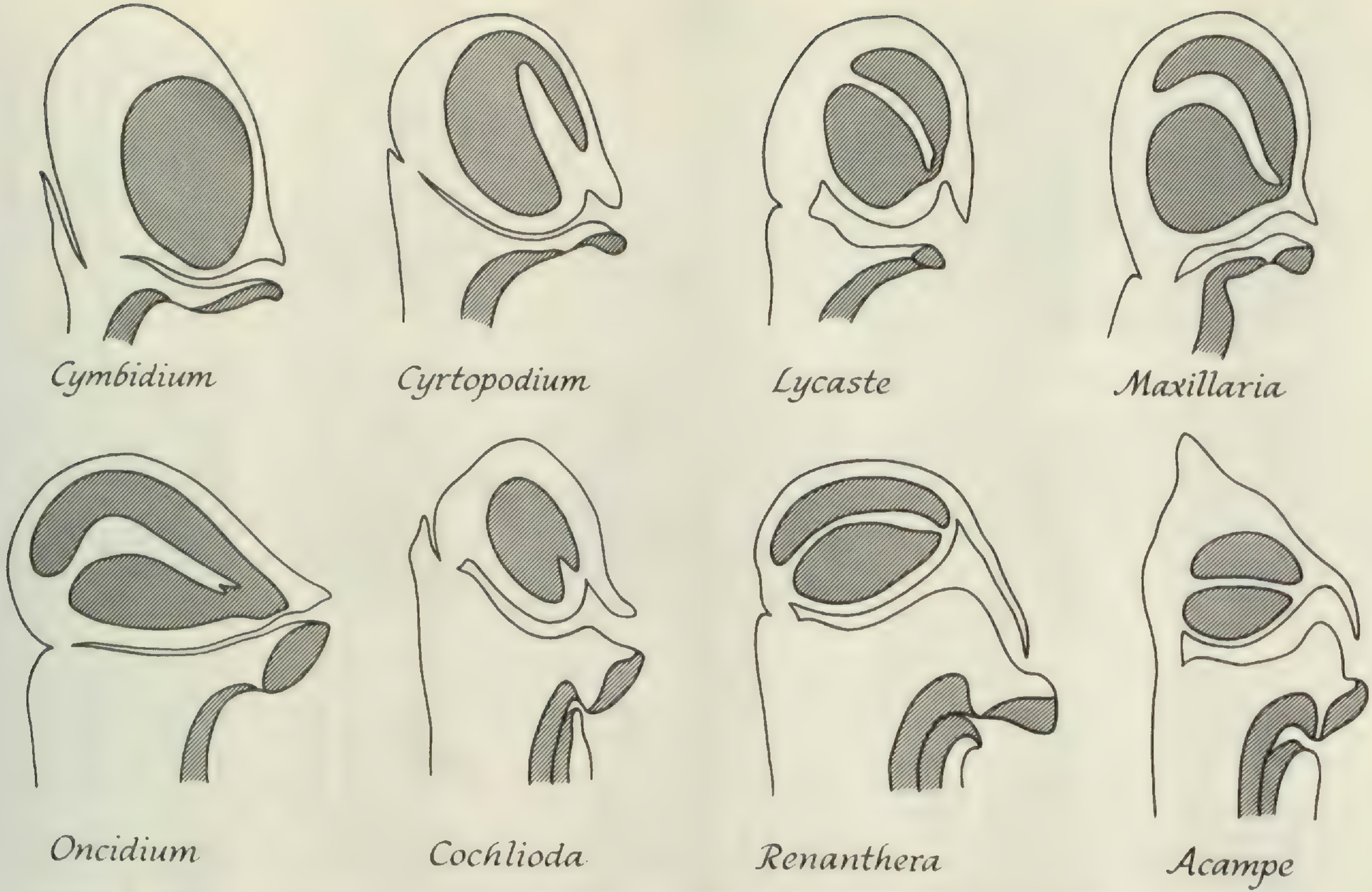

FIGURE 6. Diagrammatic median longitudinal sections of column in developing buds of members of tribe VANDEAE.

place in the early history and origin of the NEOTTIOIDEAE. Embryological evidence favors such a proposition, for the primitive type of embryo with a single-celled suspensor is found only in members of the Cranichideae and in the less evolved species of the Epidendreae. The evolutionary success of the EPIDENDROIDEAE, however, is due primarily to the development of the epiphytic mode of life, as has already been mentioned (6).

EVOLUTIONARY PERSPECTIVES

The family Orchidaceae originated in the area known phytogeographically as Malaysia during the Cretaceous period when most angiospermous families became differentiated. At that time all species were geophytes, for the epiphytic mode of life is a rather recent development, dating back to the Pliopleistocene. While the terms geophytic and epiphytic convey the meaning of ecological habitats, in reality they express distinct evolutionary adaptations through morphological modifications in the roots. In the terrestrial roots, which may be thin and fibrous or thick and fleshy, the epidermis consists of one to three layers of cells, the outermost layer being provided with root hairs. In the derived epiphytic roots, the layers of epidermal cells are greatly increased in number into a spongy velamen with the outermost layer cutinized and devoid of root hairs. Hence the structure of the root and not the place of abode differentiates these two types of evolutionary adaptations, the latter one of which is also an evolutionary innovation.

There is no other plant family comparable in floral diversity to the Orchidaceae. The basic trimerous pattern common to most monocotyledons, displays such a vast array of modifications in this family that without serious study one could question the validity of calling them all orchids. Yet, all of the flowers have three sepals and alternating with them three petals, the unpaired petal greatly modified into a labellum or lip, an evolutionary adaptation providing a landing platform for pollinating insects. In the center of the flower, ordinarily occupied by the style and encircled by alternating rows of stamens, all orchids possess a novel structure called the gynostemium or column. The column is also an evolutionary innovation, the result of fusion of the style with the filaments of various stamens.

Concurrently with the development of the column two additional evolutionary innovations became operational. The first is the development of pollinia, in which the pollen grains at the time of maturity are shed either as free single grains, or variously aggregated into tetrads or massulae. Each of these phases is very characteristic for a given subfamily (4, 5, 6). The manner in which the individual grains are united into tetrads or massulae is a unique feature of the orchid family, for the interfaces among the grains instead of becoming separated by an exine layer remain connected through cytoplasmic plasmodesmata. Because of this phenomenon cytogenetically deficient grains are brought to maturity, and in turn can affect fertilization (1). This condition is amply demonstrated by the

occurrence of large aneuploid series, a source of variation, especially in the subfamily EPIDENDROIDEAE and the more advanced members of the NEOTTIOIDEAE (5, 6).

The kind of pollinia, that is, the stage of the aggregation of pollen grains, is the very factor that determines the population size and the spatial distribution of the individuals of each species. In the subfamilies APOSTASIOIDEAE, CYPRIPEDIOIDEAE and NEOTTIOIDEAE both are rather limited. However, in the EPIDENDROIDEAE in the final stage of evolution of pollinia into firm, compact massulae, permitting the pollinating vectors to carry them over great distances, spatially extensive populations appear as the rule rather than the exception.

Yet, the success of this mechanism in regulating as well as maintaining the population-size is closely tied in with the second additional evolutionary innovation referred to above, namely the alteration of one of the stigmatic lobes into a new organ, the rostellum. The rostellum produces either a viscous secretion or a viscous gland to which the pollinia are attached. It is, therefore, a device that ensures successful cross pollination by firmly anchoring the pollinia to vectors for transportation. This evolutionary modification is observable in the more advanced members of the NEOTTIOIDEAE and in the subfamily EPIDENDROIDEAE. There is no rostellum in the APOSTASIOIDEAE, CYPRIPEDIOIDEAE and ORCHIDOIDEAE (6).

In addition to anchorage, the rostellum also serves as a device that prevents self pollination. In a few species, however, if the flower is not visited by a pollinator, at the end of anthesis the rostellum dries up, thus allowing the pollinia to come into contact with the stigma and permitting self pollination (5).

Orchids are pollinated by a large variety of insects, especially bees, flies, wasps, butterflies and moths, as well as by hummingbirds. Ordinarily the pollinator is species specific. Undoubtedly, cross pollination is merely a by-product of the insect's activity when attracted by a flower and stimulated to satisfy one of the ever-present dynamic urges of nature: hunger or sex. While the flowers of most orchid species provide either nectar or edible tissue as an attractant for the visiting insect, there are a few which successfully mimic the female species of the pollinator, thus attracting them sexually. Recognition of this unusual orchid-insect association which results in pseudocopulation, is a relatively recent addition to our knowledge of orchidology, yet the phenomenon itself must be of long standing in the evolutionary history of the family. Although in the annals of orchidology a large number of descriptive cases of individual pollinating mechanisms are recorded, the value of these observations and their evolutionary implications will be first realized when the mutual coaptations between flowers and insects and the reciprocal modifying influence on their evolution are convincingly demonstrated.

The evolutionary innovations discussed above, and their mutual interactions to a large extent explain the origin of, and present-day diversity within, the family. However, the dispersal of sundry orchid diaspores has played an equally important role in bringing about this diversity, especially

when it was followed by some type of isolation. The common isolating barriers among orchid species are physiological, ecological, ethological, or geographic and relatively seldom genetic. This observation is corroborated by literally thousands of artificial hybrids, often between remotely related species, as well as by the occurrence of natural hybrids. The relative frequency of natural hybrid populations of orchids in the subfamily EPIDENDROIDEAE is an additional indication of the rapid evolutionary expansion that took place within a less rigid framework than would be possible with genetic incompatibility as a controlling force. Hybridity whether natural or artificial can occur only within a given subfamily. The lack of genetic compatibility between species belonging to different subfamilies, even in artificially attempted crosses, seems to support the thesis that the kladogenetic differentiation into five subfamilies must indeed have taken place shortly after the family came into existence (6).

Closely associated with the initial kladogenetic differentiation of the orchid family is its early expansion and global dispersal. Continental distribution patterns are usually intimately associated with the geologic, climatic, and edaphic history of a given area, hence their explanation is rarely problematic. Transoceanic dispersals, on the other hand, are more perplexing, for the causes often are hidden in the evolutionary past of our biosphere (7).

There are approximately 800 genera recognized in the orchid family, and of these only 32 can now be identified as being involved in some kind of oceanic distribution. It is significant that 27 of the 32 taxa, i.e. 85 percent, are genera whose members are exclusively terrestrial. Epiphytic orchids are less habitat-specific in the microenvironment than terrestrials, yet we know only two such genera, *Bulbophyllum* and *Polystachya*, with a pantropical range. This situation, however, does not suggest that terrestrials are more effectively dispersed than epiphytes; it merely indicates that the initial transoceanic expansion must have taken place shortly after the family became established and before the epiphytic mode of life evolved. Since all of the early species were terrestrials, the transoceanic dispersal of epiphytes, although following the same route as the terrestrials did, was of much later occurrence. The necessity of mycorrhizal association is a well-known factor in orchids, but this association is not species specific. This requirement is more readily met in soil conditions where an ample supply of decaying organic matter is available than on exposed branches of trees. Hence, this is another contributing factor accounting for the rather sparse transoceanic dispersal of epiphytes (7).

Orchid genera, whether restricted to adjacent continents or pantropical in range, have the origin of their phyletic affinities in Malaysia (4, 5, 7): this center of origin must not be confused with the actual center of distribution, since the two types of centers may not be identical. In general the migratory expansion or dispersal proceeded from an easterly to westerly direction from Malaysia-India-Madagascar-Africa to Africa-South America. The exception to this is the transpacific route between Malaysia and South America as exemplified by the genera *Tropidia* and *Erythrodes*.

The migratory routes through which the various orchid dispersals were accomplished are amply documented in the pages of phytogeographical literature. They rather convincingly demonstrate that dispersals took place via oceanic routes by island-hopping rather than through supposed continental highways. There is no definite evidence that land connections of a continental nature were in existence during the Tertiary, when most of the transoceanic dispersals took place. Furthermore, geomorphological and oceanographic evidence indicates that the earth is in a constant flux and was even more so in the past. The subsidence of the ocean floor and the fluctuation of the sea level during the various geological periods, combined with orogenic activities in the earth's crust, have provided time and again favorable avenues between continents for transoceanic dispersals by means of island-hopping. In addition to these factors, wind currents have also played an important role in the transportation of orchid diaspores. In that, the "intertropical convection current" (doldrums) must have at least partially aided the realization of transoceanic distributions, for the observed distribution patterns of orchids, for instance, that of *Liparis nervosa*, and that of the intertropical convection current coincide remarkably well (7).

EPILOGUE

In spite of our attempt to view the progressive evolution of the *Orchidaceae* from a transpecific level, it always took place within specific levels. Theoretically, along the path of progressive differentiation, the newly formed types or species were much improved over their ancestors. However, even if we admit Darwin's statement that all "recent species have proved their superiority over their extinct ancestors by their survival," we must remember that this superiority does not necessarily represent progressive evolution, i.e., anagenesis. During the process of specialization, natural selection usually causes progressive adaptation to special conditions of the environment and this adaptiveness may turn into a fatal disadvantage in future development, because of the lack of ability to cope with radical environmental changes. It is for this absence of general versatility that lines with progressive specialization are frequently and ultimately doomed to extinction, notwithstanding the "superiority" of each subsequent type over the ancestral form.

The story of the evolution of the orchid family is deeply anchored in this phenomenon of extinction concerning which the present-day species with their great diversity, highly specialized and modified structures, and genetic complexities afford us only a dim view.

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CYTOMORPHOLOGY OF ARBORESCENT MORACEAE

A. S. HANS

THE FAMILY MORACEAE is comprised of 53 genera and 1400 species (Willis, 1966), distributed in tropical and warmer parts of the world with a few taxa in the temperate zone. Kanji Lal *et al.* (1940) describe 11 genera and about 60 species from Assam alone, one of the areas of the present investigation. The Moraceae exhibit variety in habit from herbaceous climbing and epiphytic to giant arborescent forms. The family is important from the point of view of forestry. The species of *Morus* L. and *Artocarpus* Forst. produce timbers in Asia, while *Piratinera guianensis* Aubl.[1] is a valuable timber of South America. Other economic products are rubber from *Castilloa elastica* Cerv. and *Ficus elastica* Roxb., fruits from *Artocarpus incisa* L.f., *Ficus carica* L., and species of *Morus* L., paper from *Broussonetia papyrifera* (L.) Vent. and species of *Streblus* Lour., and yellow dye from *Chlorophora tinctoria* D. Don. The leaves of *Morus alba* L. are the staple food of silk worms in the silk producing countries.

The knowledge of chromosome number, morphology, basic number, meiotic behavior, extent and nature of polyploidy, biology of flowering and fruiting of the desired species, and the probable morphological, eco-geographical, and cytological races of these species is essential for a breeding program for amelioration of forest trees. This paper deals with the cytomorphology of important timbers and their related species of the family Moraceae, and is a part of a larger project dealing with cytomorphological investigations of Himalayan timbers.

MATERIALS AND METHODS

The research material was collected from wild populations near Darjeeling (eastern Himalayas), Digboi (Upper Assam), and Shillong (Khasia and Jaintia hills). The male catkins, receptacles, or flower buds were fixed in Carnoys fluid and then transferred to 95 percent alcohol. The anthers were squashed in 1 percent acetocarmine and the slides were made permanent in Euparal. The somatic chromosome number in *Ficus* species was worked out from leaf tips by the oxyquinoline technique of Tjio and Levan (1950). Camera lucida drawings were made at a magnification of 2700 × from temporary slides and reduced to half the magnification while photostating. Photomicrographs were taken at a magnifica-

[1] The correct name for this seems to be *Brosimum guianense* (Aubl.) Huber, since *Brosimum* has been conserved over *Piratinera*. — *Ed.*

TABLE 1. List of the investigated taxa with their localities, cytological data, and results of previous authors

TAXON	LOCALITY AND COLLECTOR'S NUMBER	CHROMOSOME NUMBER AND LEVEL OF PLOIDY	PREVIOUS REPORT
1. *Artocarpus chaplasha* Roxb.	Digboi: Upper Dehing Reserve Forest 150 m.; *159*	$n = 28$, tetraploid	
2. *A. gomezianus* Wall.	Digboi: Upper Dehing Reserve Forest, 150 m.; *156*	$n = 28$, tetraploid	
3. *A. heterophyllus* Lam. (cultivated)	Digboi: Charali, 150 m.; *136*	$n = 28$, tetraploid	$n = 28$ (Nanda, 1962), $2n = 56$ (Le Coq, 1963)
4. *A. lakoocha* Roxb.	Digboi: Jeypore, 150 m.; *140*	$n = 28$, tetraploid	$2n = 56$ (Banerji and Hakim, 1954)
5. *Broussonetia papyrifera* (L.) Vent. (cultivated)	Darjeeling: Sukna, 150 m.; *52*	$n = 13$, diploid	$2n = 26$ (Bowden, 1940)
6. *Ficus altissima* Bl.	Darjeeling: Rongtong, 300 m.; *3118*	$2n = 26$, diploid	$2n = 26$ (Krause, 1931)
7. *F. benjamina* L. var. *comosa* Kurz	Darjeeling: Rongtong, 300 m.; *3167*	$2n = 26$, diploid	
8. *F. elastica* Roxb.	Darjeeling: Reyang, 200 m.; *3121*	$2n = 26$, diploid	$2n = 26$ (Sugiura, 1936; Condit, 1964)
9. *F. hookeri* Miq.	Darjeeling: Cart Road, 1900 m.; *3182*	$2n = 26$, diploid	
10. *F. lepidosa* Wall.	Digboi: Shillong Road, 150 m.; *3101*	$2n = 26$, diploid	
11. *F. mysorensis* Heyne	Darjeeling: Ging, 1200 m.; *10*	$2n = 26$, diploid	$2n = 26$ (Condit, 1928)
12. *F. nemoralis* Wall. var. *trilepis* (Miq.) King	Darjeeling: Gandhi Road, 1900 m.; *107*	$2n = 26$, diploid	
13. *F. religiosa* L.	Darjeeling: Peshoke, 900 m.; *3139*	$2n = 26$, diploid	$2n = 26$ (Condit, 1933)
14. *F. roxburghii* Wall.	Darjeeling: Ging, 1200 m.; *102*	$2n = 26$, diploid	
15. *Morus alba* L. (cultivated)	Darjeeling: Sukna, 150 m.; *3116*	$n = 14$, diploid	$2n = 28$ (Tahara, 1910; Osawa, 1920; Delay, 1947; Janaki Ammal, 1948)
16. *M. australis* Poir.	Darjeeling: Ging, 1200 m.; *3114*	$n = 14$, diploid	$n = 14$ (Datta, 1954; Das, 1961)
17. *M. laevigata* Wall. (cultivated)	Digboi: Nongpoh, 550 m.; *197*	$n = 28$, tetraploid	$2n = 28$ (Janaki Ammal, 1948)
	Darjeeling: Lopchu, 1500 m.; *293*		$2n = 56$ (Datta, 1954),
	Nainital: Dogaon, 2300 m.; *1217*	$n = 14$, diploid	$n = 28$ (Das, 1961)
18. *Pseudostreblus indica* Bur.	Shillong: Barapani, 1200 m.; *178*	$n = 14$, diploid	
19. *Streblus asper* Lour.	Shillong: Shella, 300 m.; *221*	$n = 13$, diploid	$n = 13$ (Gajapathy, 1961)

tion of 1350 ×. The voucher specimens are deposited in the Herbarium, Botany Department, Panjab University, Chandigarh, India.

OBSERVATIONS

The exact locality and cytological data of the 19 taxa investigated are summarized in TABLE 1. The genera and the species are arranged alphabetically. A brief description of important taxa is given below.

Artocarpus Forst.: Comprised of lofty evergreen trees with about 60 species in Indo-Malaya and China. Out of five Indian species, *A. hirsutus* Lam., *A. chaplasha* Roxb. and *A. lakoocha* Roxb. are timbers of commercial importance (Pearson & Brown, 1932).

Artocarpus chaplasha Roxb.: A large tree with an average girth of 4.5 meters and 15 to 18 meter clear bole. It is a handsome tree in Assam and Bengal where the soil is rich. In the tropical evergreen forests of upper Assam it is one of the chief elements in the upper story of the *Dipterocarpus-Mesua* formation. Its chief associes are *Amoora wallichii* King, *Endospermum chinense* Benth., *Stereospermum personatum* Chatt., *Tetrameles nudiflora* R. Br., *Cinnamomum cecidodaphne* Neisn., and *Duabanga grandiflora* (Roxb. ex DC.) Walp. It is never gregarious but found scattered in mixed plain forests of Bengal and the foothills of Assam. Bark grayish-brown, exfoliating into pieces.

MALE RECEPTACLES: March to April. FRUITING RECEPTACLES: June to September.

Artocarpus gomezianus Wall. ex Trecul: A rare tree of Tenasserim and Tavoy (Hooker, 1885; Gamble, 1902). It occurs in Assam and the Andamans (Bor, 1953). This species is quite common in the Lakhimpur district of upper Assam where it grows with a straight and cylindrical stem having at least a 10 meter clear bole. Bark gray, dull red inside, splitting into round flakes.

MALE RECEPTACLE: March. FRUITING RECEPTACLE: April to June.

Artocarpus lakoocha Roxb.: A large tree, distributed from Kumaon eastwards up to Burma. It is found scattered in Bengal and Assam, where it grows to a height of about 30 meters, with a 9 meter clear stem. Bark dark gray, peeling off into small, round, woody plates.

MALE RECEPTACLE: February to May. FRUITING RECEPTACLE: June to August.

Broussonetia papyrifera (L.) Vent.: A fast growing moderate-sized tree, indigenous to China and Upper Burma, and introduced in India. It does well on both the aspects of forest from 150 to 1500 meters in the

eastern Himalayas and Khasia and the Jaintia Hills. Brandis (1874) remarks "This useful tree seems to accommodate itself readily to different conditions of climate, and might advantageously be cultivated in North-West India."

FLOWER: February to March. FRUIT: April to May. Plants of this species are strictly dioecious.

Ficus Tourn. ex L.: The largest genus of the family Moraceae embraces trees, shrubs, climbers, and epiphytes in the tropics and subtropics of both hemispheres; and is most abundantly represented in the islands of the Indian Archipelago and the Pacific Ocean. The number of species in the genus is estimated to be from 600 to 1500 (Condit, 1964). Out of 60 Indian species, 43 are found in Assam and Khasia and Jaintia Hills. In spite of the large number of species and their widespread distribution, the genus is not of much economic importance. Only three species of some importance are mentioned by Pearson and Brown (1932) from India.

Ficus elastica Roxb. ex Hornem.: A gigantic tree in the outer hills of the eastern Himalayas from Nepal eastwards in Assam, Khasia and Jaintia hills, and Burma. Lofty trees grow near Tista (150 m.) in the Darjeeling hills and Pakyong (1000 m.) in Sikkim where they were planted for exploitation of India rubber.

RIPE FRUIT: July to September.

Morus L.: Includes about 12 species (Rehder, 1940), distributed in the temperate and subtropical regions of the northern hemisphere. Four species are met in India, of which three species produce valuable timbers.

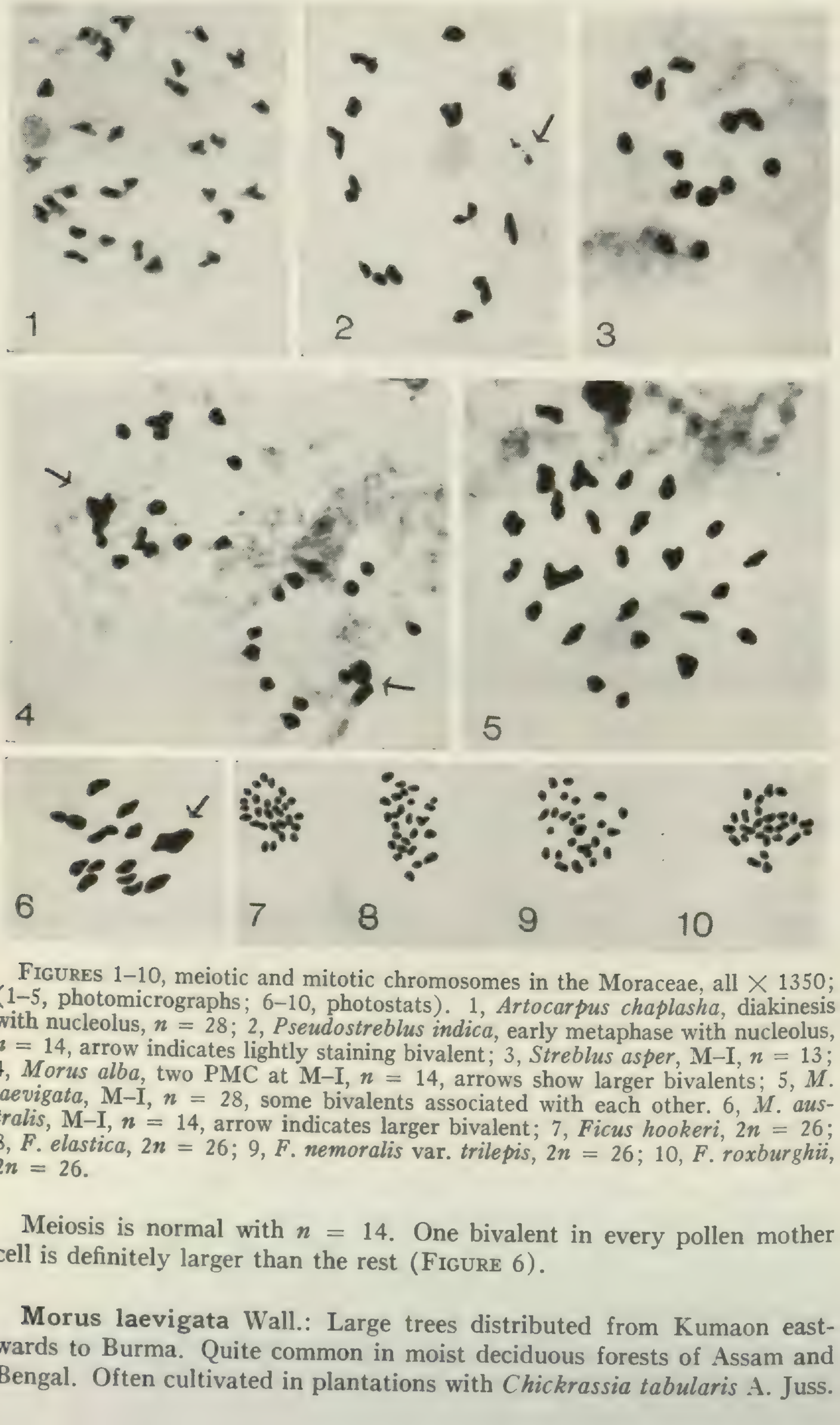
Morus alba L. Indigenous to China and now naturalized in western Asia. It is found in tropical and subtropical Himalayan tracts from Kashmir to Sikkim, and Burma. Extensively cultivated in northern India.

FLOWER: April. FRUIT: May. Male and female catkins on the same tree.

Meiosis is normal with $n = 14$. In every pollen mother cell, there are one or two larger bivalents than the rest (FIGURE 4).

Morus australis Poir. (= *M. acidosa* Griff., *M. indica* L.): moderate-sized, fast growing, deciduous tree; from Kashmir to Sikkim in the subtropical and temperate Himalayas. This species has been cultivated for a long time and has become naturalized in many parts of India. Bark brown, blaze dull white.

FLOWER: March. FRUIT: April to May. This species is strictly dioecious, the male trees being rare in comparison to the female.



FIGURES 1–10, meiotic and mitotic chromosomes in the Moraceae, all × 1350; (1–5, photomicrographs; 6–10, photostats). 1, *Artocarpus chaplasha*, diakinesis with nucleolus, $n = 28$; 2, *Pseudostreblus indica*, early metaphase with nucleolus, $n = 14$, arrow indicates lightly staining bivalent; 3, *Streblus asper*, M–I, $n = 13$; 4, *Morus alba*, two PMC at M–I, $n = 14$, arrows show larger bivalents; 5, *M. laevigata*, M–I, $n = 28$, some bivalents associated with each other. 6, *M. australis*, M–I, $n = 14$, arrow indicates larger bivalent; 7, *Ficus hookeri*, $2n = 26$; 8, *F. elastica*, $2n = 26$; 9, *F. nemoralis* var. *trilepis*, $2n = 26$; 10, *F. roxburghii*, $2n = 26$.

Meiosis is normal with $n = 14$. One bivalent in every pollen mother cell is definitely larger than the rest (FIGURE 6).

Morus laevigata Wall.: Large trees distributed from Kumaon eastwards to Burma. Quite common in moist deciduous forests of Assam and Bengal. Often cultivated in plantations with *Chickrassia tabularis* A. Juss.

TABLE 2. **Comparison of diploid and tetraploid races of Morus laevigata**

CHARACTER	DIPLOID ($n = 14$)	TETRAPLOID ($n = 28$)
Habit and distribution	Small to medium-sized trees in W. Himalayas, not common.	Middle to large tree in E. Himalayas, quite common.
Branch	Slender, slightly hairy.	Stout, hairy.
Leaf	100–130 × 50–70 mm., very slightly hairy.	140–190 × 80–120 mm., hairy.
Male catkin	Up to 60 mm., sparsely hairy.	Up to 110 mm., hairy.

at 700 m. and with *Alnus nepalensis* D. Don at 1500 m. The species grows to 25 m. in the eastern Himalayas and up to 15 m. in the western Himalayas.

FLOWER: March. FRUIT: April to May.

Two cytotypes seem to exist, one diploid with $n = 14$ (Janaki Ammal, 1948; B. S. Gill, personal communication) in the western Himalayas, and the other tetraploid with $n = 28$ (Datta, 1954; Das, 1961) in the eastern Himalayas. The cytotypes differ morphologically in certain characteristics (TABLE 2) except in size of stomata and pollen grains where the differences are negligible. My thanks are due to Dr. B. S. Gill who kindly lent his specimens from Nainital (eastern fringes of the W. Himalayas, or rather the central Himalayas) making possible the comparison between the cytotypes (FIGURE 11).

Pseudostreblus indica Bur.: Medium-sized trees with restricted distribution in the evergreen climax forests of Surma Valley of Assam and Khasia and Jaintia hills (Barapani forest, 1200 m.). Bark greenish-gray with a few scattered warts.

FLOWER: May to June. FRUIT: November to January.

Meiosis is normal. One of the bivalents is invariably more lightly stained than the rest (FIGURE 2).

Streblus asper Lour.: A medium-sized evergreen tree in the sub-Himalayan tract from Beas eastwards up to Burma, and also in the Andaman Islands. Bark grayish white and warty.

FLOWER: March to April. FRUIT: May to June.

This species is strictly dioecious and the frequency of occurrence of male trees is greater than the female ones.

DISCUSSION

The prevalent base numbers in the Moraceae are 13 and 14 (Darlington & Wylie, 1955). A great majority of the species are diploid. Poly-

FIGURE 11. Two cytotypes of *Morus laevigata*. A, tetraploid ($n = 28$), from Khasia and Jaintia hills, and eastern Himalayas. B, diploid ($n = 14$), from western Himalayas (male catkin broken).

ploidy is of rare occurrence in the genus *Ficus*. Condit (1964) reports seven tetraploid species of *Ficus* and one triploid, in the horticultural variety 'Decora' of *F. elastica*. Of the known species, about 8 percent are polyploid. The genus *Morus* is predominantly diploid except for a few natural or artificially raised polyploid species. All the four presently investigated species of *Artocarpus* are tetraploid. Perusal of literature reveals only one species (*A. cannoni*) to be polyploid.

Diploid ($n = 14$) and natural tetraploid ($n = 28$) races of *Morus laevigata* occur in the western and eastern Himalayas respectively. A comparison of these cytotypes reveals that the tetraploid is of greater height, more hairy, has larger leaves, and longer male catkins than the diploid. The size of the stomata and pollen grains is almost the same in the two races.

Das (1961) reports the occurrence of multivalents, laggards and irregular separation of chromosomes in the tetraploid *Morus laevigata*, thereby inferring an imbalanced state of polyploidy. The present findings show normal meiosis and almost 100 percent pollen fertility in specimens from various localities at different altitudes. Some bivalents have the tendency to associate with each other, but do not necessarily result in multivalent formation. It is possible that induction of polyploidy in this

species is recent and that some of the individuals are still in the "floating" state.

The presence of one or two larger bivalents in *Morus alba* and *M. australis* was noted by previous workers. Tahara (1909) found two large chromosomes in these two species and labelled them "alpha" and "beta." Osawa (1920) after investigating seven species and 85 races of *Morus*, concluded that there was in every case one large pair per diploid complement. The irresistible interpretation of the large chromosomes occurring in unisexual trees could be as sex chromosomes. Sinoto (1929) infers that the unequal pair in *M. bombycis* corresponds to the XY mechanism and consequently the males are heterogametic in regard to sex, but adds that they are not directly related to sex in the sense that the effect of them is not seen in the phenotype. The present investigations reveal in fact quite the reverse situation. The larger bivalent(s) is noticed in the pollen mother cells of *M. alba* where both male and female catkins were present on the same plant, thus ruling out the possibility of their being sex chromosomes. Schaffner (1936) has reported spontaneous sex reversal in *M. alba*. Plants destined to be unisexual, bear catkins of the other sex as well. Progeny obtained by selfing these flowers is either unisexual or bisexual. He infers that unisexuality in *Morus*, or to be precise, in *M. alba* is not affected by hereditary differentials like the XY allosome set, but by physiochemical or physiological variables, both male and female individuals being potentially bisexual.

SUMMARY

Nineteen woody species of the Moraceae from the eastern Himalayas, the Khasia and Jaintia Hills, and Upper Assam were investigated cytomorphologically. *Pseudostreblus* (*P. indica*, $n = 14$) is the genus worked out for the first time. The other taxa reported chromosomally for the first time are *Artocarpus chaplasha*, *A. gomezianus* (both with $n = 28$), *Ficus benjamina* var. *comosa*, *F. hookeri*, *F. lepidosa*, *F. nemoralis* var. *trilepis*, and *F. roxburghii* (all with $2n = 26$).

Morus laevigata has two cytotypes, one diploid ($n = 14$) in the western Himalayas, and the other tetraploid ($n = 28$) in the eastern Himalayas, which differ in respect to habit, hairiness, and dimensions of leaves and male catkins. The dioecious condition in *Morus* is not governed by an XY allosome set, but by some yet unknown physiochemical or physiological factors.

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THE PHRYMACEAE IN THE SOUTHEASTERN UNITED STATES [1]

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PHRYMACEAE Schauer in A. P. de Candolle, Prodr. **11:** 520. 1847.
(LOPSEED FAMILY)

A monotypic family [2] of herbaceous dicotyledons distinguished by perfect, hypogynous, zygomorphic flowers; synsepalous calyx with the 3 upper lobes subulate and hooked; sympetalous 2-lipped corolla; 4 epipetalous stamens; pseudomonomerous gynoecium with a basal orthotropous to hemianatropous ovule; and an achene enclosed in the accrescent calyx. TYPE GENUS: *Phryma* L.

The Phrymaceae are of somewhat uncertain taxonomic status. They are regarded as allied most closely to the Verbenaceae, differing principally in the solitary ovule and the superior radicle. In stem anatomy, *Phryma* is similar to "certain members" of the Verbenaceae (Smith). According to Lipscomb, in general vegetative form, inflorescence type, and flower and fruit anatomy *Phryma* has its closest affinities with the tribe Lantaneae of the Verbenaceae and is structurally most similar to the genus *Stachytarpheta*; she favors tribal status for *Phryma* in the Verbenaceae. Other authors (Baillon; Bentham & Hooker; Hutchinson, 1926) have included *Phryma* among the Verbenaceae, but it is more commonly treated as the sole genus of a distinct family.

The Phrymaceae, along with the Globulariaceae and *Littorella* and

[1] Prepared for a generic flora of the southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of the National Science Foundation (Grant GB–6459X, principal investigator Carroll E. Wood, Jr.). This treatment follows the format established in the first paper in the series (Jour. Arnold Arb. **39:** 296–346. 1958). The area covered includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. References that I have not seen are marked with an asterisk.

I am indebted to Dr. Wood for his careful review of the manuscript and for other aid; to Ralph Andrews and Fran Uhler for data on wildlife use of *Phryma*; and to the curators of herbaria who responded to my request for distributional data on *Phryma*. The illustration was made by Rachel A. Wheeler from dissections by Dr. Wood.

[2] *Melananthus* Walpers was originally described as a second genus of the Phrymaceae. Its systematic position was considered doubtful by Bentham & Hooker. Later, Taubert reaffirmed the affinity between it and *Phryma*. Finally, on anatomical and morphological grounds, Solereder transferred the genus to the Solanaceae, tribe Salpiglossideae.

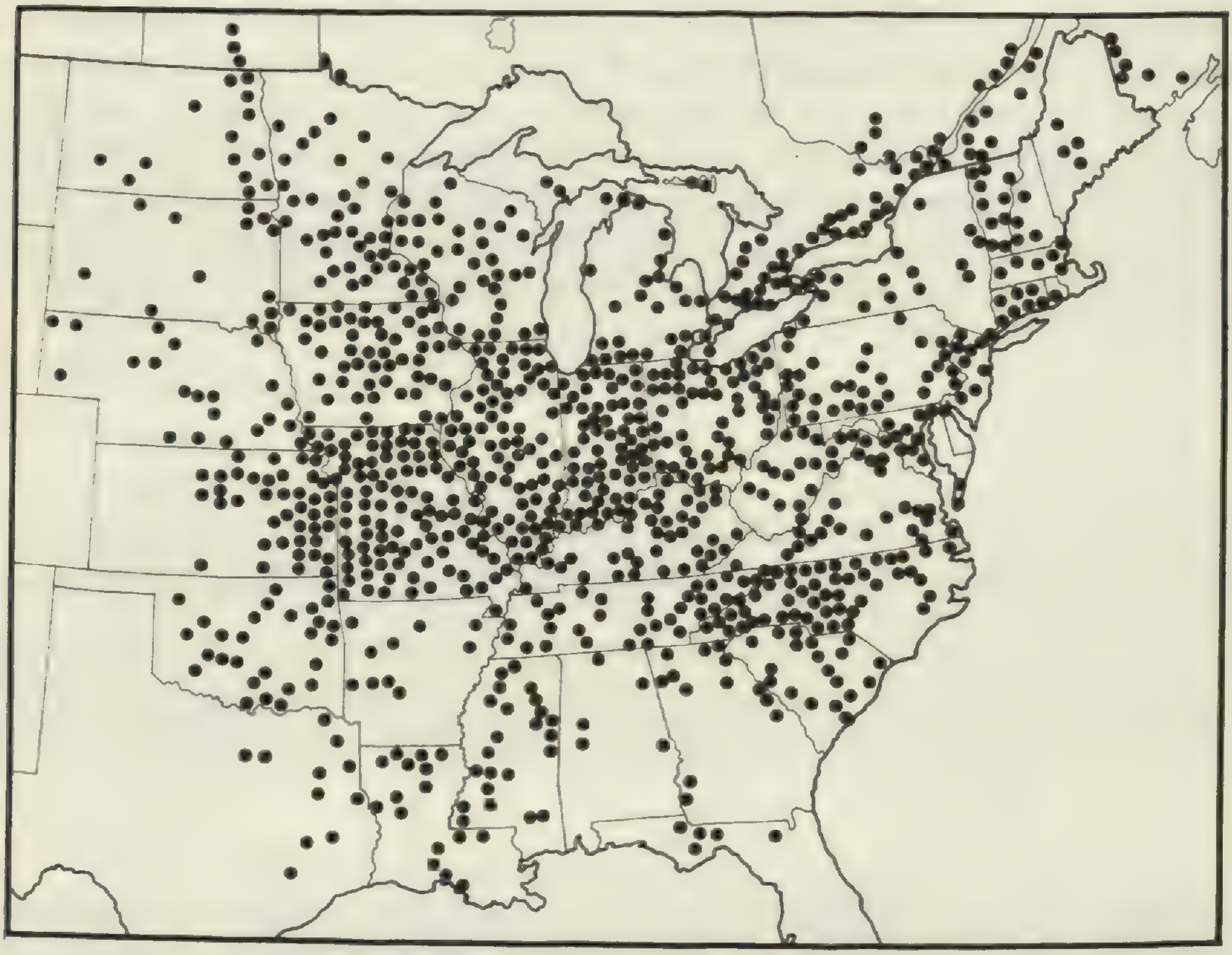
Bougueria of the Plantaginaceae, provide good examples of pseudomonomerous gynoecia (Eckhardt, Wilson & Just). Such a gynoecium, actually a syncarpous structure, has the appearance of a single carpel; it develops through suppression of all but one of the original carpels. In *Phryma*, the gynoecium is viewed as being two-carpellate, with one carpel (the posterior?) being reduced. Lipscomb found the gynoecium to be "bicarpellate as indicated by two dorsal bundles which extend the length of the pistil."

1. **Phryma** Linnaeus, Sp. Pl. 2: 601. 1753; Gen. Pl. ed. 5. 262. 1754.

Simple or branched perennial herbs. Leaves opposite, simple, serrate to crenate-serrate, the lower long-petioled, the upper nearly sessile. Inflorescences of terminal, long-peduncled, spikelike racemes. Flowers perfect, zygomorphic, hypogynous, axillary to bracts, horizontal at anthesis,

FIGURE 1. **Phryma.** a–h, *P. leptostachya* var. *leptostachya*: a, upper part of small plant with flowers and young fruit, × 3/8; b, flower, × 4; c, corolla laid open, × 4; d, anther, × 20; e, gynoecium in vertical section to show ovule, × 15; f, nearly mature fruiting calyces, × 4; g, fruit, × 5; h, embryo, × 5.

sharply reflexed soon thereafter, opposite or sometimes the lower ones alternate, the pedicels short, bibracteolate. Calyx persistent, synsepalous, cylindrical, strongly zygomorphic, 2-lipped, the upper lip of 3 subulate, hooked lobes about equalling the tube at anthesis, the lower much shorter, of 2 triangular lobes, the tube sulcate, accrescent in fruit. Corolla sympetalous, the tube cylindrical, the limb 2-lipped, the upper lip upwardly diverging, notched, external in the bud, the lower lip much longer, horizontally projecting, 3-lobed, the palate uparching, 2-ridged centrally. Androecium didynamous, the stamens included, alternate, epipetalous, the



Documented distribution of *Phryma leptostachya* in North America. For map of approximate distribution in Asia (var. *oblongifolia*) see Trans. Am. Philos. Soc. II. 42: 422. 1952.

lower pair the longer; filaments elongate; anthers dorsifixed, 4-sporangiate, 2-locular at anthesis, the locules dehiscing longitudinally; pollen 3-colpate, subprolate. Gynoecium syncarpous, pseudomonomerous, 2-carpellate; stigma 2-lobed, the upper lobe the shorter; style 1, elongate, slender, included; ovary unilocular, with 1 basal ovule; ovule orthotropous (Cooper) to hemianatropous (Lipscomb), unitegmic, tenuinucellar. Fruit a narrowly ellipsoid achene included in the accrescent, closed calyx that is tipped by the 3 indurated, hooked, upper lobes; seed filling the fruit, endosperm thin (2 cell layers), the embryo with convolute cotyledons. Embryo sac development normal (Polygonum type); radicle superior; endosperm *ab initio* cellular, with a 4-celled chalazal haustorium. TYPE SPECIES: *P. leptostachya* L. (Derivation of the name unknown.[3]) — LOPSEED.

A genus of a single species with bicentric distribution in mesic to moist, deciduous or mixed forests of eastern North America and southeastern Asia. *Phryma leptostachya* L. ranges in the New World, as var. *leptostachya*, $2n = 28$, from New Brunswick to Wisconsin, extreme southwestern Ontario, and southwestern Manitoba south to western Nebraska, eastern Texas, and northern Florida, and as var. *confertifolia* Fern. (of

[3] Kuprianova asserts that *Phryma* is a native Amerindian name.

dubious taxonomic significance), from eastern Virginia to Delaware;[4] and in Asia, as var. *oblongifolia* (Koidz.) Honda (var. *asiatica* Hara, *P. asiatica* (Hara) Degener & Degener), $2n = 28$,[5] from the Himalayas to Manchuria, southeasternmost Soviet Union (Primorski Krai), Japan, and North Vietnam (Tonkin). The Asiatic plants differ only slightly from the American ones, mainly in pubescence, length of the upper calyx lobes, shape of the upper corolla lip, and often smaller corollas (Hara).

The flowers open at various times during the day or night, but usually in the morning. In bud they are ascending, but as anthesis approaches they gradually become horizontal. Usually both flowers of a pair open more or less at the same time, but occasionally one may open as much as 36 hours after its mate. Anthesis typically proceeds regularly up the raceme, although sometimes a pair may open a full day before the pair below it. Individual flowers last 12–36 hours, after which the corolla drops, and within 24–48 hours the flower becomes sharply reflexed. After anthesis, the calyx tube (but not the lobes) increases in size and the three upper lobes become indurated.

The corolla is white, with the upper lip and sometimes the lower one strongly pink tinged. The calyx tube and lower lobes are green, but the upper lobes are either the same shade as or a pink darker than that of the corolla.

The flowers of *Phryma* are strongly proterandrous. According to Robertson, pollination is accomplished by long-tongued insects, including *Halictus purus* (*Augochlora pura*), a mining bee; short-tongued insects are excluded from the corolla tube by the up-arching palate, although small bees can force their way into it. In spite of several hours spent watching plants of *Phryma* at various times of day and night (on South Bass Island, Ottawa County, Ohio) the author never saw an insect visiting one.

The disseminules are the indehiscent fruits enclosed in the accrescent calyx tube. Three of the calyx lobes are much longer than the other two and are hooked apically. Dispersal is presumably epizoöchorous (Ridley). Dispersal in the fur of animals apparently has not been demonstrated, but hooking onto clothing can take place.

An extract of the leaves and roots of *Phryma* has been found to possess insecticidal properties. The active principle, phrymarol, is evidently a "kind of sterine" (Kikutani & Oshima). In the lower Yangtze Valley, the Chinese name of *P. leptostachya* means "poisonous fly-plant" (Steward), and in Japan the plant "is used to kill the common houseflies" (Matsuzawa).

The fruits of *Phryma* are known to be eaten by wild turkeys in Virginia.

[4] *Phryma* was collected about a century ago in Bermuda, but "probably only as a waif" (Britton).

[5] Darlington & Wylie's assertion (Chromosome atlas of flowering plants, p. 323. 1955) that Sugiura (Cytologia 7: 587. 1936) reported a diploid number of 14 for *P. leptostachya* is erroneous; he reported a *haploid* number of 14. This same error is repeated by Bolkovskikh, Grif, Matvejeva, & Zakharyeva (Chromosome numbers of flowering plants, p. 486. 1969).

Among the fungi that parasitize *Phryma* are two, *Puccinia extensicola* var. *phrymae* (*Aecidium phrymae*) and *Septoria leptostachya*, the names of which commemorate their host.

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2. TROPICOS: names, types,

A REVISION OF THE NEOTROPICAL GENUS LISIANTHIUS (GENTIANACEAE)

#0006878

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TAXONOMIC TREATMENT

Lisianthius P. Browne, Civ. Nat. Hist. Jamaica 157. *t. 9.* 1756.

Lisianthus L. Mant. Pl. 43. 1767.
Leianthus Griseb. Gen. & Sp. Gent. 196. 1839 [1838], *nom. illegit.* [Art. 63].
Petasostylis Griseb. in DC. Prodr. **9:** 71. 1845.

Plants short-lived, coarse, perennial suffrutescent herbs or subshrubs, spindly shrubs, or even small trees, very rarely annual herbs, usually glabrous but occasionally puberulous; often monopodial, but occasionally with several main axes. Roots tufted, fibrous, often woody. Stems terete, but with 2 pairs of raised parallel ridges on opposite sides, these usually obscured below, the pairs sometimes diverging and the stems then 4-angled. Leaves opposite, entire or rarely papillate or ciliolate, membranaceous or more rarely moderately coriaceous, the venation obscure or prominent on the lower surface of the leaf, of 1–2 pairs of primary lateral veins, when 2 pairs, the lower originating near the base of the blade, the upper closely paralleling the midvein for a distance before diverging, all ultimately curving to the leaf margin and closely paralleling it; petioles winged or not, or leaves sessile, the bases of the pairs fused, forming a sheath around the stem. Inflorescences often terminating the main stem and the upper lateral branches, the entire upper portion of the plant appearing as a single, large, diffuse inflorescence, equally often axillary or on modified lateral, leafy, determinate shoots, and then never terminating the main axis, or very rarely solitary flowers in the axils of the foliage leaves; basically branched systems of compound dichasia with the ultimate branches often monochasial, but frequently reduced and the dichasia appearing simple; inflorescence branches long and the inflorescences open, or branches contracted and the inflorescences dense and compact, rarely branches practically nonexistent and inflorescences appearing capitate or umbellate; bracts subtending the dichasia foliaceous but different in shape and reduced in size from the foliage leaves, or equally often greatly reduced and essentially scarious; flowers usually pedicellate, rarely sessile, the lateral pedicels in each dichasial unit subtended by a pair of opposite or subopposite bracteoles, these scarious or rarely foliaceous. Flowers nodding or horizontal, more rarely erect or ascending.

* Continued from volume 53, p. 100.

Calyx chlorophyllous, fused to the middle or more commonly only near the base, the inner surface of the tube covered to varying degrees with minute digitate squamellae; lobes 5, long acuminate or rarely acute, usually with scarious margins, often carinate or even alate abaxially. Corolla marcescent and frequently persisting on the mature, dehisced capsule, usually with conspicuous fibrous bundles visible as longitudinal whitish lines when dried, tubular-funnelform (or tubular or tubular-campanulate), very rarely salverform; lobes ovate-lanceolate or oblong-lanceolate (broadly ovate or even suborbicular), usually acuminate but rarely acute or obtuse, erect, spreading, or recurved. Stamens 5, usually inserted in the lower third of the corolla tube, only very rarely inserted in the throat, nearly always surpassing the corolla tube and occasionally surpassing the lobes; filaments elongate, filiform, expanded at the base and abruptly upturned at the apex, usually unequal in length, rarely subequal; anthers oblong, the connective slightly exserted or not, yellow (or purple). Pistil 2-carpellate; ovary oblong-ellipsoid or rarely ovoid, unilocular or bilocular, when unilocular the septum incomplete usually only at the base, the placentae scarcely protruding into the lumen of the ovary; style filiform, usually exceeding the corolla lobes, always longer than the filaments and usually exceeding them; stigma capitate or peltate, bilobed (often indistinctly), the lobes hemispherical. Capsule gray-brown, sometimes glaucous when immature, surrounded by the persistent calyx and marcescent corolla which often falls off before the seeds are shed, typically fusiform or oblong-ellipsoid, rarely ovoid, beaked, with the placentae, upon dehiscence, visible as whitish, erose bands along the margins of the valves adjacent to the suture. Seeds numerous, very small, angular, densely pitted with numerous small depressions. ✓LECTOTYPE SPECIES: *L. longifolius* L., chosen by Britton & Wilson, Sci. Surv. Porto Rico VIRGIN Is. 6:84. 1925.

KEY TO THE SECTIONS OF LISIANTHIUS

Corolla greenish or greenish-white, salverform, short, the tube 1.5 cm. or less in length; stamens inserted near the apex of the corolla tube, filaments of equal length in a given flower, very short, less than 9 mm. long. . . . . I. OMPHALOSTIGMA.

Corolla, at least the tube, yellow, red, or "black," tubular or funnelform, the tube more than 1.8 cm. long and usually much longer; stamens inserted in the lower 1/3–1/2 of the corolla tube; filaments of unequal length in a given flower, more than 10 mm. long and usually much longer. . . . . II. LISIANTHIUS.

I. **Lisianthius** sect. **Omphalostigma** (Griseb.) Weaver, comb. nov.

Leianthus sect. *Omphalostigma* Griseb., pro parte, Gen. & Sp. Gent. 198. 1839 [1838].

Annual or perennial herbs, glabrous or minutely spiculate. Inflorescences terminal and axillary on the primary and secondary shoots, basically of compound dichasia. Corolla salverform, the limb widely flaring, greenish

or greenish-white, small, the tube 15 mm. long or less. Stamens inserted near the apex of the corolla tube, the filaments equal in one flower, less than 9 mm. long. Sculpturing of pollen grains reticulate. LECTOTYPE SPECIES: *L. saponarioides* Cham. & Schlecht.

The section OMPHALOSTIGMA was defined more or less tentatively by Grisebach (1839) in his genus *Leianthus* to include the two Mexican species known at that time, *L. saponarioides* (Cham. & Schlecht.) Griseb. (= *Lisianthius saponarioides* Cham. & Schlecht.) and *L. nigrescens* (Cham. & Schlecht.) Griseb. (= *Lisianthius nigrescens* Cham. & Schlecht.). These species reputedly differed from the West Indian species then known in having peltate rather than capitate stigmas and corollas swollen at the base and narrowed above, rather than narrowed at the base.

Stigmatic type has proved to be generally unreliable as an indicator of relationships in *Lisianthius*. According to my interpretation, *L. nigrescens* belongs in the typical section of the genus. Therefore *L. saponarioides*, by exclusion of *L. nigrescens*, becomes the lectotype species of Grisebach's section. At any rate, although both *L. nigrescens* and *L. saponarioides* have peltate stigmas, only *L. saponarioides* is characterized by corollas which are swollen at the base and narrowed above, and then only in older flowers. *L. saponarioides* therefore best demonstrates the characters mentioned above as supposedly distinctive of sect. OMPHALOSTIGMA according to Grisebach, and, in any event, would be the better choice as a lectotype species.

KEY TO THE SPECIES OF LISIANTHIUS SECTION OMPHALOSTIGMA

Inflorescences compacted, the dichasia often sessile and appearing pleiochasial; calyx 5.5–10 mm. long, the lobes 4–7.5 mm. long, surpassing the ovary at anthesis; corolla 1.4–2.1 cm. long, the lobes 4–7 mm. long and cuspidate-acuminate; filaments 3–8.5 mm. long; flowers subsessile or very short pedicellate, the pedicels not more than 1 mm. long; plants glabrous or minutely spiculate, but the calyx and the midveins of the leaves always glabrous; calyx in fruit 2/3 as long to nearly as long as the capsules. . . . . 1. *L. saponarioides.*

Inflorescences diffuse, the dichasia always pedunculate and never appearing pleiochasial; calyx 3.5–5 mm. long, the lobes 2–3 mm. long, never surpassing the ovary; corolla 1.2–1.7 cm. long, the lobes 2.5–4.5 mm. long and acute or rarely short acuminate; filaments 2–4 mm. long; flowers distinctly pedicellate, the pedicels 2–4 mm. long; plants minutely spiculate, including the calyx tube and the midveins of the leaves; calyx in fruit usually 1/3 and never more than 1/2 as long as the capsule. . . . . 2. *L. meianthus.*

1. **Lisianthius saponarioides** Cham. & Schlecht. Linnaea 6: 389. 1831 (as *Lisianthus*). TYPE. **Mexico.** VERACRUZ: Ad margines sylvarum Papantlae, *Schiede* (HAL!).

Leianthus saponarioides (Cham. & Schlecht.) Griseb. Gen. & Sp. Gent. 198. 1839 [1838].

Petasostylis saponarioides (Cham. & Schlecht.) Griseb. in DC. Prodr. **9**: 71. 1845.

Lisianthus congestus Standl. Carnegie Inst. Publ. **461**: 82. 1935. TYPE. **Guatemala**. PETÉN: Sabana de San Francisco, La Libertad, *Lundell 2479* (F!).

Rather coarse, erect, monopodial, perennial (?) herbs, glabrous or minutely spiculate. Stems 8–14 dm. tall, green, minutely spiculate (with magnification) or more rarely essentially glabrous, terete below but 4-angled above, the angles usually minutely serrulate. Leaves (1.6)3.2–12 cm. long and (0.7)1.3–4 cm. broad, dull textured on both surfaces, papillose above and with the margins of the upper leaves often very minutely ciliolate, the lateral veins inconspicuous below; the principal foliage leaves narrowly elliptic (or ovate-lanceolate), long-acuminate, long-attenuate at the base, essentially sessile or with a short, winged petiole to 3 mm. long; the upper leaves and those on the secondary branches distinctly ovate or ovate-lanceolate, rounded or subcordate at the base, distinctly short-petiolate. Inflorescences of sessile or pedunculate dichasia, these usually 1–2(–4) times compound but often reduced and appearing simple, borne singly or in groups of 3, the terminal one often sessile and the whole unit appearing pleiochasial; inflorescence branches usually contracted and the dichasia or groups of dichasia dense and compact, more rarely somewhat elongate and the dichasia more diffuse, 4-angled, 2 of the angles often expanded into scarious wings, minutely spiculate; bracteoles scarious, subulate. Flowers erect or ascending, subsessile or very short pedicellate, the pedicels not exceeding 1 mm. in length. Calyx 5.5–10 mm. long, fused for 2/10–3/10 its length; the lobes 4–7.5 mm. long and 1–1.5 mm. broad, lanceolate, long-acuminate, scarious margined, ridged abaxially; the tube 1.5–2.5 mm. long. Corolla 1.4–2.1 mm. long, salverform, greenish-white or green; the tube at anthesis narrow, 10–15 mm. long and ca. 1.5 mm. in diameter, conspicuously white-striate at least at the base; the lobes 4–7 mm. long and 2–4.5 mm. broad, flaring and recurved, ovate-lanceolate or more rarely somewhat elliptic, long-acuminate, conspicuously longer than broad, usually 1/3 as long as the tube but varying from 3/10–4/10 as long. Stamens inserted near the apex of the corolla tube, in the upper 1/6–1/3, at or just above the apex of the calyx lobes; filaments subequal, (3)4.5–7.5(8.5) mm. long, surpassing the corolla tube but not the lobes, usually surpassing the style; anthers 1.5–2.5 mm. long and ca. 1 mm. broad, oblong, becoming almost sagittate upon dehiscence. Style 6–10 mm. long, surpassing the corolla tube; stigma peltate. Capsule oblong-ellipsoid, 5–10 mm. long and 3–4 mm. broad; the marcescent corolla apparently not persisting until the seeds are shed. FLOWERING: All year.

DISTRIBUTION: From 600 to 1200 meters on rocky limestone hillsides and in secondary scrub from the State of Veracruz, Mexico, south and east to Chiapas, the departments of Huehuetenango and Petén, Guatemala, and western British Honduras (MAP 1).

REPRESENTATIVE COLLECTIONS

Mexico. CHIAPAS: Laguna Ocotal Grande, ca. 25–30 km. se. of Cerro Líbano, *Dressler 1481* (IJ, MEXU, US). VERACRUZ: ad margines sylvarum Papantlae, *Schiede & Deppe s.n.* (BM). **Guatemala.** HUEHUETENANGO: cafetal of Finca Soledad, 5 mi. se. of Barillas, Sierra de los Cuchumatanes, *Steyermark 49547* (F). PETÉN: La Cumbre, w. of km. 139 of Cardenas Road, *Contreras 6205* (F); Lake Petén Itza, 2 km. s. of Santa Elena, on La Cueva Road, *Contreras 2060* (LL); Sabana San Francisco, La Libertad, *Lundell 2479* (MICH, isotype of *L. congestus*); Tikál, on top of Temple IV, *Contreras 166* (F, IJ, LL). **British Honduras.** CAYO DIST.: hill se. of Millionario, *Proctor 29820* (DUKE, IJ); near Camp 6, *Gentle 2363* (A, F, LL, NY).

Lisianthius saponarioides is a rather poorly collected plant of which only 28 specimens were available for study. With their small, greenish, salverform corollas and short stamens inserted near the apex of the corolla tube, *L. saponarioides* and *L. meianthus* form a very distinctive group unlikely to be confused with any other species in the genus.

Despite its distinctiveness, *Lisianthius saponarioides* has had a rather confused history. Until recently, the name usually was applied incorrectly to plants recognized here as *L. acuminatus* and *L. quichensis*, both morphologically very different from *L. saponarioides*. The reason for the confusion is unclear. Chamisso and Schlechtendal, in the original description of *L. saponarioides*, describe the corolla as ". . . *hypocrateriformis, tubo tertia circiter parte calycem superans* . . ." Certainly no other species in the genus, known then or now, is characterized by having a salverform corolla with the calyx reaching to 2/3 of the length of the corolla tube.

Grisebach (1839, 1845) evidently applied the name correctly (as *Leianthus saponarioides*, 1839, and *Petasostylis saponarioides*, 1845). Hemsley (1882) cited *Sumichrast 1558*, a fragment of this collection now the lectotype of *L. acuminatus* Perk., as representative of *L. saponarioides*. Gilg (1895) included a figure of a plant (p. 92, *Figure 41–A*) which he called *L. saponarioides*, but which undoubtedly represents *L. acuminatus* Perk., a fact recognized and pointed out by Perkins (1902, p. 493). However, Perkins (*loc. cit.*, p. 491) cited *Heyde & Lux 2921*, from Dept. Quiché Guatemala, as representative of *L. saponarioides*. *Heyde & Lux 2921* superficially resembles *L. acuminatus* much more than it does *L. saponarioides*. The specimen of *Heyde & Lux 2921* (US) was later selected by John Donnell Smith as the holotype of *L. quichensis*.

Although Williams (1968, 1969) considered *Lisianthius congestus* Standl. to be synonymous with *L. saponarioides*, he did it with some reservation. I have seen the holotypes of both *L. congestus* and *L. saponarioides*; they are similar in all respects and undoubtedly represent the same taxon.

There was no correctly determined material of *Lisianthius saponarioides* in American herbaria in 1935 when Standley described *L. congestus*. Therefore, in view of the confused application of the name at that time, it is quite possible that Standley did not consider *L. saponarioides* when describing his new species. He did not compare *L. congestus* to any known

species but rather stated that it is "distinguishable at once" from other Central American species "by the densely flowered, congested inflorescence."

2. **Lisianthius meianthus** Donn. Sm. Bot. Gaz. **52**: 51. 1911 (as *Lisianthus*). TYPE. **Guatemala:** Sacolal, bei Pansamalá, *von Tuerckheim 1436* (US!).

Rather coarse, annual herbs, minutely pubescent. Stems 7–14 dm. tall and to 5 mm. in diameter, erect, green, terete below but 4-angled above, minutely and densely spiculate in the upper portions. Leaves (0.7)1.5–9 cm. long and (0.3)1.3–3.5 cm. broad, dull textured on both surfaces, densely papillose above and with very minutely ciliolate margins, the midvein and the principal lateral nerves conspicuous below, minutely spiculate; principal foliage leaves lanceolate or ovate-lanceolate, rarely tending toward elliptic, long-acuminate, attenuate at the base, essentially sessile or with short, winged petioles to 2 mm. long; the upper leaves and those on the secondary branches distinctly lanceolate, rounded or subcordate at the base, distinctly short-petiolate. Inflorescences of distinctly pedunculate dichasia, these usually 1–2 times compound but often reduced and appearing simple, borne singly or in groups of 3, the ultimate branches often scorpioid; inflorescence branches elongate and the dichasia or groups of dichasia loose and open, 4-angled, densely spiculate. Flowers ascending or horizontal, the pedicels 2–4 mm. long and minutely spiculate; bracteoles subulate, scarious. Calyx 3.5–5 mm. long, fused for 3/10 — nearly 1/2 its length; the lobes 2–3 mm. long and ca. 1 mm. wide, lanceolate, acuminate, scarious-margined, ridged abaxially; the tube 1–2 mm. long, minutely spiculate. Corolla 12–16.5 mm. long, salverform; the tube at anthesis narrow, 9–12.5 mm. long and ca. 1.5 mm. in diameter at the base, greenish, conspicuously white-striate at least at the base; the lobes flaring, 2.5–4.5 mm. long and 1.5–2.5 mm. broad, oblong-oblanceolate or oblong-elliptic, acute or rarely short-acuminate, longer than broad, 1/3–1/5 as long as the tube. Stamens inserted near the apex of the corolla tube, in the upper 1/5, well above the apex of the calyx lobes; filaments subequal 2–4 mm. long, surpassing the corolla tube, equalling or slightly exceeding the style; anthers ca. 1.5 mm. long and 1 mm. broad, oblong, becoming almost sagittate upon dehiscence. Style 5–8 mm. long, surpassing the corolla tube; the stigma peltate. Capsule oblong-ellipsoid, beaked, 6–9 mm. long, not including the 1–3.5 mm. long beak, and 2–4 mm. in diameter; the marcescent corolla not persisting until the seeds are shed. FLOWERING: Oct.–Apr.

DISTRIBUTION. From near sea level to 1500 meters in pine forests, limestone thickets, and along roadsides in central, southern, and eastern Guatemala (MAP 1).

SPECIMENS EXAMINED

Guatemala. ALTA VERAPAZ: Saquíja, 45 km. ne. of Cobán, *Standley 70166* (NY, F); between Cobán and Finca Chimoté, near Rubeltein, *Steyermark 44179*

(F); woods between Finca Gubilguitz and Hacienda Yaxcabanal, *Steyermark 44821* (F, NY). IZABAL: along Highway CA–9 near turnoff to Mariscos, *Weaver 2186* (DUKE); between milla 49.5 and ridge 6 mi. from Izabal, Montaña del Mico, *Steyermark 38534* (GH, F). SUCHITEPEQUEZ: Finca Moca, *Skutch 1568* (F, US).

A very poorly collected species, *Lisianthius meianthus* is the only one in the genus definitely known to be an annual.

Lisianthius meianthus is similar to *L. saponarioides* and was combined with it by Williams (1968, 1969). As outlined in the key, *L. meianthus* differs from *L. saponarioides* in having the principal veins of the leaf (lower surface) and the calyx tube spiculate; an open loose inflorescence; pedicels at least 2 mm. long; calyx shorter and never equalling the ovary; and the corolla lobes shorter, and acute or short-acuminate. These differences are constant and diagnostic, and all of the available specimens are easily assignable to one taxon or the other.

Whether the two taxa, *L. meianthus* and *L. saponarioides*, are specifically or only varietally distinct is perhaps open to question. Until more complete collections are available for both, I prefer to treat *L. meianthus* and *L. saponarioides* as distinct species.

II. Lisianthius section Lisianthius.

Subshrubs, shrubs, or slender trees, more rarely suffrutescent, perennial herbs, very rarely annual, glabrous or puberulous. Inflorescences terminal and axillary on primary and secondary shoots, or on specialized determinate flowering branches, of compound or apparently simple dichasia, more rarely reduced to single flowers. Corolla tubular or funnelform, the limb erect, spreading, or recurved, the tube yellow, or more rarely red or black. Stamens inserted in the lower 1/3–1/2 of the corolla tube, the filaments of unequal length in a given flower, more than 10 mm. in length, usually much longer. TYPE SPECIES: *L. longifolius* L.

This, by far the larger section, may be divided into two subsections, based primarily on differences in habit.

KEY TO THE SUBSECTIONS OF LISIANTHIUS SECTION LISIANTHIUS

Perennial, suffrutescent, very rarely annual, herbs, dying back to the woody base after each flowering season; plants monopodial, the main axis determinate; branching excurrent; inflorescences typically of compound dichasia, terminal and axillary on the primary and secondary shoots, never reduced to solitary axillary flowers; capsules ovoid or more rarely oblong-ellipsoid; principal foliage leaves sessile and usually clasping; corolla tube yellow, red, or black. ..... **A. subsect. HERBACEI.**

Subshrubs, shrubs, or slender trees, persisting for more than a single season; plants not monopodial, the main axes branched above, at least in older plants, the branches indeterminate; branching seldom excurrent; inflorescences of apparently simple dichasia, rarely of compound dichasia and either axillary or axillary and terminal on determinate lateral shoots, occasionally reduced to

solitary, axillary flowers; capsules oblong-ellipsoid or fusiform; principal foliage leaves petiolate (or subsessile), never clasping; corolla tube yellow or very rarely red. ..... B. subsect. FRUTICOSI.

Lisianthius sect. **Lisianthius** subsect. **Herbacei** Weaver, subsect. nov.

Herbae perennae suffrutescentes, grossae monopodiales, raro herbae annuae, omnino glabrae. Ramificatio excurrens. Folia sessilia plerumque amplexicauliaque. Dichasia vulgo composita, terminalia axillariaque. Capsulae ovoideae vel raro oblongo-ellipsoideae. SPECIES TYPICA: *L. nigrescens* Cham. & Schlecht.

The species in subsect. HERBACEI, in contrast to those in subsect. FRUTICOSI, are suffrutescent herbs with terminal inflorescences. One of them, *Lisianthius silenifolius*, is possibly an annual. Six of the seven species are distributed in Mexico and Guatemala, the remaining one, *L. silenifolius*, in Cuba.

KEY TO THE SPECIES OF SUBSECTION HERBACEI

A. Corolla tube dull red; corolla lobes obtuse and somewhat erose, very rarely acute; calyx fused for 1/3–1/2 its length, fleshy, the lobes narrowly ovate, acute or short-acuminate, completely ecarinate; anthers purple. ..... 9. *L. viscidiflorus*.

A. Corolla tube yellow or black; corolla lobes acuminate or more rarely acute; calyx fused for 1/4 its length or less, not fleshy, the lobes lanceolate, long-acuminate or more rarely acute, ridged or carinate abaxially; anthers yellow.
  B. Corolla lobes ovate to squarish or suborbicular, less than twice as long as broad, 2–4 mm. long, 1/10–1/8 as long as the tube; corolla narrowly tubular; inflorescences congested or rarely diffuse, the dichasia often sessile and appearing pleiochasial; inflorescence branches strongly winged; stamens inserted on the corolla tube ca. 1/2 the distance from the base to the apex. ..... 8. *L. brevidentatus*.
  B. Corolla lobes ovate-lanceolate or lanceolate, more than twice as long as broad, (3)5–24 mm. long, more than 1/5 as long as the tube; corolla broadly tubular or funnelform; inflorescences diffuse, the dichasia never sessile or appearing pleiochasial; inflorescence branches terete or indistinctly 4-angled, very rarely with narrow, scarious wings; stamens inserted on the corolla tube ca. 1/3 of the distance from the base to the apex.
    C. Corolla black; capsules ovoid or fusiform.
      D. Capsules fusiform; inflorescence branches distinctly 4-angled, the angles expanded into narrow, scarious wings, these minutely serrulate; inflorescences of apparently simple dichasia, very rarely of compound dichasia; leaves dull green and papillose on the upper surface, weakly clasping at the base; corolla lobes more than 1/2–3/4 as long as the tube; stamens inserted below the apex of the calyx lobes; styles seldom surpassing the midpoint on the corolla lobes. ..... 3. *L. cuspidatus*.
      D. Capsules ovoid and often broadly so; inflorescence branches terete or indistinctly 4-angled, the angles not serrulate or expanded into

narrow scarious wings; inflorescences of compound dichasia, rarely of apparently simple dichasia; leaves glossy and not papillose on the upper surface, strongly clasping at the base; corolla lobes usually 1/6–1/2 as long as the tube, very rarely more than 1/2 as long; stamens inserted above the apex of the calyx lobes; styles nearly always equalling or surpassing the corolla lobes. . . . . 4. *L. nigrescens*.

C. Corolla yellow; capsules ovoid and usually broadly so.

E. Foliage leaves rounded or truncate at the base, clasping; corolla lobes spreading or recurved; corolla tube not at all inflated, widest at the apex; styles not surpassing to conspicuously surpassing the corolla lobes.

F. Corolla lobes recurved, 11–20 mm. long, more than 1/3 as long as the tube; calyx 9–15 mm. long; style equalling to conspicuously surpassing the corolla lobes; plants of Mexico. . . . . 5. *L. oreopolus*.

F. Corolla lobes spreading, 5.5–9 mm. long, less than 1/3 as long as the tube; calyx 6–11.5 mm. long; style never surpassing the corolla lobes; plants of Cuba. . . . . 6. *L. silenifolius*.

E. Foliage leaves narrowed at the base, not clasping; corolla lobes erect; corolla tube slightly inflated, widest below the apex; styles always surpassing the corolla lobes. . . . . 7. *L. quichensis*.

3. **Lisianthius cuspidatus** Bertol. Nov. Comm. Bonon. **4**: 408. *t. 37*. 1840 (as *Lisianthus*). TYPE. **Guatemala,** without exact locality, *Velásquez*, presumably at Bologna (BOLO) but not seen.

Leianthus cuspidatus (Bertol.) Griseb. in DC. Prodr. **9**: 82. 1845.
Lisianthus nigrescens var. *cuspidatus* (Bertol.) L.O. Wms. Fieldiana Bot. **31**: 408. 1968.

Rather coarse, perennial herbs. Stems 0.7–3 m. tall and to 1 cm. in diameter, erect or ascending, green or often purplish, terete below and 4-angled above, the angles expanded into narrow, scarious wings. Leaves (0.9)2.4–10.1 cm. long and (0.1)0.4–2.7 cm. broad, firmly membranaceous, the margins minutely papillose, the principal foliage leaves lanceolate or more rarely ovate-lanceolate, long-acuminate, narrowly tapered to rounded at the base, weakly clasping, the base usually less than twice the diameter of the stem; upper leaves and those on the secondary branches lanceolate, the bases rounded or cuneate, short-petiolate or sessile but not clasping. Inflorescences composed of dichasia, usually 2–3-flowered and appearing simple, rarely 1-compound, long-pedunculate; inflorescence branches strongly 4-angled, elongate and the inflorescences appearing loose and open. Flowers drooping, long-pedicellate, the pedicels 0.5–2.2 cm. long; bracteoles subulate, scarious. Calyx 10–14.5 mm. long, fused for 1/6–1/5 its length; the lobes 8–12 mm. long, lanceolate, long-acuminate, scarious-margined, ridged abaxially; the tube 1.5–2.5 mm. long. Corolla funnelform, uniformly black, 4–5.6 cm. long; the tube 2.6–3.3 cm. long and 7–8 mm. in diameter at the apex; the lobes 1.4–2.4 cm. long and 3–5 mm. broad, spreading and slightly recurved at the tips, lanceolate or oblong-

lanceolate, long cuspidate-acuminate, 1/2–3/4 as long as the tube. Stamens inserted on the corolla tube ca. 1/3 of the distance from the base to the apex; filaments 1.8–2.9 cm. long, only slightly surpassing the corolla tube; anthers oblong, 2–2.5 mm. long and 1–1.5 mm. broad. Style 2.1–2.9 cm. long, surpassing the corolla tube but not reaching to more than the midpoint on the corolla lobes; stigma peltate. Capsule fusiform, beaked, 1.1–1.5 cm. long, not including the 1–2 mm. long beak, and 3–5 mm. in diameter; the marcescent corolla seldom persisting until the seeds are shed. FLOWERING: Aug.–Nov.

DISTRIBUTION: In pine forests about 2000 meters elevation in central Guatemala (MAP 2).

SPECIMENS EXAMINED

Guatemala: without locality, *Bernoulli 320* (NY); without locality, *Bernoulli & Cario 1804* (S); San Martín, *Johnston s.n.* (F). EL PROGRESSO: Sierra de las Minas, Finca el Bucaral, 14 km. from the highway from Salamá to El Rancho, *Hawkes, Hjerting & Lester 1968* (F, S); between Calera and middle slopes of quebradas on Volcán Siglo, *Steyermark 43001* (F, NY). GUATEMALA: in the Sapoie barranca near Guatemala, *Hayes s.n.* (GH); San Juan Sacatepéquez, *Lewis 895* (F). QUICHÉ: without locality, *Aguilar 1400* (F).

Lisianthius cuspidatus is a poorly collected species; only eleven specimens were available for study. It is quite similar to *L. nigrescens* var. *chiapensis*, especially in its black corollas.

I have not seen Bertoloni's type, or any authentic material known to have been in his possession when the original description was made. However, his diagnosis and the plate accompanying it are perfectly adequate and leave no doubt as to the plant he had at hand.

The relationship of *Lisianthius cuspidatus* to *L. nigrescens*, the other black-flowered species, has been the subject of considerable debate since *L. cuspidatus* was originally described. Grisebach (1845) and Robinson (1910) considered the two as distinct species. In fact Grisebach even placed them in different genera, *cuspidatus* in *Leianthus* and *nigrescens* in *Petasostylis*. Hemsley (1882), Kuntze (1891), and Perkins (1902) reduced *L. cuspidatus* to synonymy under *L. nigrescens*. Williams (1968, 1969) treated *L. cuspidatus* as a variety of *L. nigrescens*. His *L. nigrescens* var. *cuspidatus*, as discussed later, included plants here treated as *L. nigrescens* var. *chiapensis* and *L. cuspidatus*.

Williams (1968) felt that the characters used by Robinson (1910) to separate *Lisianthius cuspidatus* from *L. nigrescens*, i.e. the subcuneate leaf bases, the more deeply lobed corolla, and the corolla lobes distinctly surpassing the style "begin to lose their significance with more adequate collections." My observations would lead me to disagree with Williams; although there is a small overlap in lobe/tube ratio between *L. cuspidatus* and *L. nigrescens* (var. *chiapensis*), the other characters hold quite well. In addition the 3-flowered dichasia, serrulate stem angles, dull-textured, papillose leaves, and especially the fusiform capsules clearly set *L. cuspi-*

Maps 1–3. Distribution of *Lisianthius* species. Map 1, *L. meianthus* (dots), *L. saponarioides* (triangles). Map 2, *L. cuspidatus* (triangles), *L. nigrescens* var. *nigrescens* (dots), *L. nigrescens* var. *chiapensis* (half-circles). Map 3, *L. brevidentatus* var. *brevidentatus* (dots), *L. brevidentatus* var. *collinus* (half-circle), *L. oreopolus* (squares), *L. quichensis* (triangles).

datus apart from *L. nigrescens*. I think that the differences between the two taxa are of sufficient magnitude to warrant maintaining *L. cuspidatus* as a distinct species.

4. **Lisianthius nigrescens** Cham. & Schlecht. Linnaea 6: 388. 1831 (as *Lisianthus*).

Coarse, perennial herbs. Stems 0.5–2 m. tall and to 2 cm. in diameter, erect or ascending, green except at base, terete below but indistinctly 4-angled above. Leaves firmly membranaceous, the lateral veins prominent, the principal foliage leaves 3–19 cm. long and 1–6.4 cm. broad, ovate-lanceolate or elliptic or sometimes rather oblong or even somewhat pandurate, gradually or abruptly acuminate, the bases truncate and auriculate, distinctly clasping, much broader than the stem, the upper leaves and those on the secondary branches smaller, lanceolate or ovate, rounded at the base, short-petiolate or sessile but not clasping. Inflorescences of long-pedunculate dichasia, these 1 to 4 times compound, the lateral branches often scorpioid, or sometimes reduced and appearing simple; inflorescence branches terete or indistinctly 4-angled, elongate with the dichasia appearing loose and open. Flowers horizontal or nodding, the pedicels (0.3)0.6–3.0(4.0) cm. long; bracteoles subulate, scarious. Calyx (6)7.5–13.5 mm. long, fused for 1/8–1/4 its length; the lobes (4.5)7–11 mm. long, and 1.5–2.5 mm. broad, lanceolate, long-acuminate, scarious-margined, carinate or at least ridged abaxially. Corolla funnelform, uniformly black, glossy outside and dull within, 3.2–5.4 cm. long; the tube 2.7–3.9 cm. long and 4–7 mm. in diameter at the apex; the lobes 0.5–1.6(2.0) cm. long and 2–4 mm. broad, 1/6–1/2(3/5) as long as the tube, lanceolate or ovate-lanceolate, gradually short-acuminate or rather long cuspidate-acuminate, spreading, recurved only at the tips if at all. Stamens inserted on the corolla tube ca. 1/3 of the distance from the base to the apex; filaments 2.1–3.4 cm. long, exceeding the corolla tube and frequently the lobes, the longest ones equalling the style or not; anthers 2–3.5 mm. long and 1–2 mm. broad, broadly oblong, truncate or obtuse at the apex, the connective very slightly if at all exserted. Ovary ovoid; style 2.1–4.5 cm. long, exserted, not at all to conspicuously exceeding the corolla lobes. Capsules ovoid and frequently broadly so, 7–13 mm. long and 3–6 mm. broad; the marcescent corolla strongly persisting until after the seeds are shed.

Key to the Varieties

Corolla lobes 9 mm. or less in length, gradually short-acuminate; filaments, at least the longest ones, usually surpassing the corolla lobes; styles always surpassing the corolla lobes, and often conspicuously so. . . . . 4a. *L. nigrescens* var. *nigrescens*.

Corolla lobes 9–20 mm. long, but usually more than 11 mm., long cuspidate-acuminate; filaments never surpassing the corolla lobes; styles at most equal-

ling or barely surpassing the corolla lobes. . . . . 4b. *L. nigrescens* var. *chiapensis*.

4a. **Lisianthius nigrescens** Cham. & Schlecht. var. **nigrescens.**

Lisianthius nigrescens Cham. & Schlecht. Linnaea **6:** 388. 1831 (*as Lisianthus*). ✓TYPE. **Mexico.** VERACRUZ: in sylvis Papantla, *Schiede* (HAL!).

Leianthus nigrescens (Cham. & Schlecht.) Griseb. Gen. & Sp. Gent. 199. 1839 [1838].

Petasostylis nigrescens (Cham. & Schlecht.) Griseb. in DC. Prodr. **9:** 71. 1845.

Corolla 3.2–4.6 cm. long, the lobes lanceolate, gradually short-acuminate, 5–8(9) mm. long and 2–3 mm. broad, 1/6–1/4 as long as the tube. Filaments 2.1–3.3 cm. long, at least the longest ones in each flower equalling or surpassing the corolla lobes. Styles 2.7–3.5(4.2) cm. long, exceeding the corolla lobes (often conspicuously), always surpassing the styles. FLOWERING: Jan.–Aug. CHROMOSOME NUMBER: $n = 18$.

DISTRIBUTION: From 800 to 1400 meters on dry rocky hillsides and on roadside banks in Veracruz, Hidalgo, and Oaxaca, Mexico (MAP 2).

REPRESENTATIVE COLLECTIONS

Mexico: without exact locality, *Sessé, Mocino, et al. 5097* (F). HIDALGO: alrededores de Huejutla, *Maury 6013* (MEXU). OAXACA: 1 km. e. of Tonaguilla, *Schultes 591* (GH); vicinity of Choapan, *Nelson 893* (GH, US). VERACRUZ: Yotoa, *Galeotti 1473* (F, GH, NY, US); Orizaba, *Purpus 1182* (F, GH, MO, NY, UC); Cerro de Escamela, on road to Ojo de Agua, just e. of Orizaba, *Weaver 2134* (A, BM, DS, DUKE, F, IJ, LL, MICH, MO, NY, S, UC, US); Papantla, *Liebmann 10787* (GH, F, MO, S, UC, US); Zacuapan, *Purpus 5994* (GH, MO, UC); from El Rancho de Sacalica to El Municipio de Zongolica, *Santos 2075* (MICH); Córdoba, *Miranda 632* (MEXU).

Williams (1969) considered *Cook 65* (US) the only known Guatemalan specimen that represents the typical variety. This specimen is intermediate in character between var. *nigrescens* and var. *chiapensis*, but is closer to the latter especially in the shape of the corolla lobes and the fact that the style does not exceed the corolla lobes.

4b. **Lisianthius nigrescens** Cham. & Schlecht. var. **chiapensis** Weaver, var. nov. TYPE. **Mexico.** CHIAPAS: 7.8 mi. e. of Chiapa de Corzo on Highway 190, *Weaver 2168* (DUKE!).

Habitu et foliis varietati typicae similis, differt lobis corollae longioribus, longe cuspidato-acuminatis, longitudine vulgo 1/2 tubi aequantibus, et stylum vix vel paulo superantibus.

Corolla 3.7–5.4 cm. long, the lobes lanceolate or ovate-lanceolate, rather long cuspidate-acuminate (9)11–16(20) mm. long and 3–4 mm. broad, 3/10–1/2(3/5) as long as the tube. Filaments 2.3–3.4 cm. long, never surpassing the corolla lobes, sometimes equalling the style. Styles 2.5–4.5 cm. long, at most equalling or very slightly surpassing the corolla lobes. FLOWERING: Apr.–Oct. CHROMOSOME NUMBER: $n = 18$.

DISTRIBUTION: From 500–1800 meters in pine and/or oak forests, secondary scrub, and along roadsides in Chiapas, Mexico, and Huehuetenango, Guatemala (MAP 2).

REPRESENTATIVE COLLECTIONS

Mexico. CHIAPAS: without exact locality, *Ghiesbreght 702* (BM, GH, MO, NY); 7.8 mi. e. of Chiapa de Corzo on Highway 190, *Weaver 2168* (A, BM, DS, F, IJ, LL, MICH, MO, NY, S, UC, US; isotypes); along Mexican Highway 190 in the Zinacantán paraje of Muctajoc, Municipio de Ixtapa, *Breedlove 11839* (DS, MEXU); at junction of Mexican Highway 190 and road to Bochil & Simojovel, Municipio de Ixtapa, *Breedlove 9600* (DS, F); ca. 30 mi. e. of Tuxtla Gutiérrez, *Webster, Miller & Miller 11699* (DUKE, MICH, MEXU); 17 km. n. of Tuxtla Gutiérrez along road to El Sumidero, Municipio de Tuxtla Gutiérrez, *Breedlove 14006* (DS, LL, MICH); along Mexico 190 at paraje Granadilla, Municipio de Zinacantán, *Laughlin 1074* (DS, LL); in paraje 'Apas, Municipio de Zinacantán, *Laughlin 1213* (DS, LL, MEXU); 2 mi. sw. of Aguacatenango junction on road to Las Rosas, *Weaver 2183* (A, BM, DS, DUKE, F, IJ, LL, MICH, MO, NY, S, UC, US); at the junction of the Pan American Highway and the road to Soyala, *Breedlove 6571* (DS, MICH); between San Ricardo & Ocozucuantla, *Nelson 2986* (US); along Mexican Highway 190, 7 mi. s. of La Trinitaria, Municipio de La Trinitaria, *Breedlove 10038* (DS, LL, MEXU). **Guatemala.** HUEHUETENANGO: Finca Candelaria, *Cook 65* (US); between San Ildefonso Ixtahuacan and Cuilco, *Steyermark 50682* (F, US).

Lisianthius nigrescens is by far the most common of the Mexican species, rather frequently encountered on roadside banks, especially in the state of Chiapas. With its black corollas, ovoid capsules, and sessile leaves with broad, clasping bases, *L. nigrescens* is easily distinguishable from most of the other species of *Lisianthius*. The only other species with black flowers is *L. cuspidatus*, which differs from *L. nigrescens* in that its leaves, though sessile and more or less clasping, are papillose above and on the margins and the bases are usually narrowed and not auriculate; its corollas are more deeply lobed; and its capsules are fusiform. *L. oreopolus* resembles *L. nigrescens* strongly in aspect, vegetative characters, and capsule shape, but differs in having uniformly yellow corollas, with the tube expanding more or less abruptly above the basal constriction, and the lobes strongly recurved.

Williams (1968, 1969) treated *L. cuspidatus* Bertol. and *L. oreopolus* Robins. as varieties of *L. nigrescens*. He pointed out (1968) that var. *cuspidatus* differs from typical *L. nigrescens* in having larger and more deeply lobed corollas, but warned that, with more adequate collections, the varieties may eventually be shown to be the same. Williams (1968) considered var. *oreopolus* to be almost identical with var. *cuspidatus* except for its yellow corollas. In this treatment *L. oreopolus*, and *L. cuspidatus*, have been retained as full species.

Williams apparently misinterpreted *Lisianthius cuspidatus*. He relied too heavily on the degree of corolla lobing as the primary character for separating it from *L. nigrescens*; he thought the differences in the leaf

bases were insignificant and was apparently unaware of the difference in capsule shape as well as the other characters listed above.

Bertoloni described *Lisianthius cuspidatus* as having oblong capsules. However, Williams (1969) included in his var. *cuspidatus* plants with the oblong (or fusiform) capsule of *L. cuspidatus* and the broadly ovoid capsules of *L. nigrescens*. According to Williams (loc. cit.) his var. *cuspidatus* is distributed in the Mexican state of Chiapas and the Guatemalan departments of Huehuetenango, Guatemala, Chimaltenango, El Progresso, and Quiché. The plants from the last four Guatemalan departments are characterized by having fusiform capsules and therefore belong to *L. cuspidatus*. The Mexican plants and those from Huehuetenango are characterized by having ovoid capsules and therefore belong to *L. nigrescens*.

Williams' var. *cuspidatus* is therefore a heterogeneous taxon, including elements of both *L. nigrescens* and *L. cuspidatus*. His figure of var. *cuspidatus* (1969, p. 325, *figure 88*) represents both elements, although this fact is not particularly obvious from the drawing. *Figure 88–A*, drawn from *Steyermark 50682* (F), represents *L. nigrescens*, and *figure 88–C*, drawn from *Hawkes, Hjerting & Lester 1968* (F), represents *L. cuspidatus*.

The specimens of *Lisianthius nigrescens* from Chiapas, Mexico, and Huehuetenango, Guatemala, mostly included in *L. nigrescens* var. *cuspidatus* by Williams (1968, 1969), differ in a number of ways from typical *L. nigrescens* from the Mexican states of Veracruz, Hidalgo, and Oaxaca. The flowers are generally larger, the corolla lobes are longer in absolute length and longer in relation to the tube, and the styles only equal or very barely exceed the corolla lobes. Although there is a small amount of overlap in these critical characters, the two forms are readily distinguishable in most cases. On the basis of available collections, it appears that their ranges are distinct. These two forms are not perfectly differentiated but the tendencies are strong indeed, and I think failure to draw a formal distinction between them would be taxonomically unsound. Therefore I have designated the large-flowered populations from Chiapas and Huehuetenango as a new variety of *L. nigrescens*. Since the new variety is nearly restricted to the state of Chiapas, I have named it *L. nigrescens* var. *chiapensis*.

Hemsley (1882) and Perkins (1902) cited an Oersted specimen (*s.n.*), supposedly of *Lisianthius nigrescens*, from Pacaca, Costa Rica. Both authors included *L. cuspidatus* in their concept of *L. nigrescens*. I have not seen the Oersted specimen, nor any other specimen of a black-flowered species from Costa Rica, and I could not make even a reasonable guess as to its true identity.

5. **Lisianthius oreopolus** Robins. Proc. Am. Acad. **45**: 398. 1910 (as *Lisianthus*). TYPE: **Mexico.** CHIAPAS: without exact locality, *Ghiesbreght 702 bis* (GH!).

Lisianthus nigrescens var. *oreopolus* (Robins.) L.O. Wms. Fieldiana Bot. **31**: 408. 1968.

Coarse, perennial herbs. Stems 1–2 m. tall and to 2 cm. in diameter, erect, green except at the base, terete below but indistinctly 4-angled above. Leaves firmly membranaceous, the lateral veins prominent, 2.5–21.4 cm. long and 0.5–4.9 cm. broad, the principal foliage leaves sessile, lanceolate or more or less oblong, short-acuminate, the bases truncate and auriculate, broad, distinctly clasping, much broader than the stem; upper leaves and those on the secondary branches smaller and narrower, the bases narrower and less distinctly or not at all clasping. Inflorescences of long-pedunculate dichasia, these 1–4 times compound, the lateral divisions often scorpioid, or rarely appearing simple; inflorescence branches terete or indistinctly 4-angled, elongate and with the inflorescences loose and open. Flowers horizontal or nodding, the pedicels 3–9.5 mm. long; bracteoles subulate, scarious. Calyx 9–15 mm. long, fused for 1/8–1/4 its length; the lobes 6.5–12.5 mm. long and 1.5–2.5 mm. broad, lanceolate, long acuminate, scarious-margined, indistinctly carinate abaxially; the tube 1.5–3 mm. long. Corolla 4–6 cm. long, tubular-funnelform, uniformly bright yellow; the tube 2.7–4.1 cm. long and 5–9 mm. in diameter at the apex; the lobes 11–20 mm. long and 3–5 mm. broad, (1/3)1/2–2/3 as long as the tube, conspicuously recurved, lanceolate or oblong-lanceolate, long cuspidate-acuminate. Stamens inserted on the corolla tube ca. 1/3 of the distance from the base to the apex. Filaments 2.5–5.1 cm. long, at least the longest ones surpassing the corolla lobes, very rarely equalling the style; anthers 2–3.5 mm. long and 1–1.5 mm. broad, broadly oblong, the apex acutish, the connective slightly exserted. Ovary ovoid; style 3.7–6.2 cm. long, exceeding the corolla lobes or rarely only equalling them; stigma peltate. Capsules broadly ovoid, short-beaked, 8–12 mm. long and 5–7 mm. broad; the marcescent corolla persisting until the seeds are shed. FLOWERING: May–Aug. CHROMOSOME NUMBER: $n = 18$.

DISTRIBUTION: From 1000 to 1800 meters in dry or rather moist pine or mixed forests or on roadside banks in eastern and southern Chiapas, Mexico (MAP 3).

REPRESENTATIVE COLLECTIONS

Mexico. CHIAPAS: slopes along the Ala Shashib River below Habenal, paraje of Mahben Chauk, Municipio de Tenejapa, *Breedlove 6477* (DS, F); in the paraje of Mahosik, Municipio de Tenejapa, *Breedlove 14852* (DS, DUKE); near schoolhouse of Pokolum, paraje of Sibanilhá, Municipio de Tenejapa, *Breedlove 11015* (DS, F, LL, MICH); in the paraje of Kulak'tik, Municipio de Tenejapa, *Breedlove 10996* (DS, F, LL, MICH); in the barrio of Ti Ha', paraje of Mahbenchoak, Municipio de Tenejapa, *Alush Shilom Ton 2267* (DUKE); near the Colonia Choro, Municipio de San Pedro Chenálho, *Alush Shilom Ton 2457* (DUKE); 3.1 mi. n. of Bochil on road to Simojovel, *Weaver 2174* (A, BM, DS, DUKE, F, IJ, LL, MICH, MO, NY, S, UC, US).

Lisianthius oreopolus has a rather restricted distribution, and has until recently been poorly collected. With its numerous, large yellow flowers it is a very striking and handsome plant. With its long, recurved corolla

lobes, ovoid capsules, and sessile, clasping leaves, it is not likely to be confused with any other yellow-flowered member of the genus.

In the original description of *Lisianthius oreopolus*, Robinson noted that the new species resembled *L. nigrescens* in habit but differed in its yellow corollas with longer and more spreading lobes. Williams (1968) reduced *L. oreopolus* to varietal status under *L. nigrescens*, stating that it is an almost exact duplicate of his *L. nigrescens* var. *cuspidatus* in corolla size and lobing. *L. oreopolus* is quite similar to *L. nigrescens*, especially var. *chiapensis*, but its flowers tend to be larger in all ways and the corolla is in general more deeply lobed. However, there is a complete overlap in all calyx and corolla measurements between the two species. The most striking difference between the two species is the color of the corolla. In addition the corolla tube of *L. oreopolus* is more or less abruptly expanded above the basal constriction and the lobes are conspicuously recurved, while the corolla tube of *L. nigrescens* is gradually expanded above the basal constriction and the lobes are merely spreading.

It seems possible that the breeding systems of the two taxa are quite different. The difference in corolla color is very striking and very probably has a marked effect on the type of pollinator attracted to the respective taxa. In addition, the anthers of *L. oreopolus* are longer exserted than those of *L. nigrescens*. The corolla lobes of *L. nigrescens* are merely spreading and the anthers are generally held within them. Access to the throat of the corolla is blocked by the anthers, and a bee seeking nectar would certainly brush against them in the process. The corolla lobes of *L. oreopolus* are recurved and the filaments project rather far from the throat of the corolla; access to the throat of the corolla is not blocked by the anthers. Unfortunately, nothing is known about the pollinators of these plants.

At any rate, *Lisianthius oreopolus* does differ consistently from *L. nigrescens*, even though the most striking difference, the color of the corolla, may be due to only a single gene difference. Until more is known of the biology of these plants, particularly their pollination systems and crossability, I prefer to treat them as distinct species.

6. **Lisianthius silenifolius** (Griseb.) Urb. Symb. Antill. 3: 334. 1902 (as *Lisianthus*). TYPE. Western **Cuba,** *Wright*, presumably at Göttingen (GOET) but not seen.

Leianthus silenifolius Griseb. Cat. Pl. Cub. 180. 1866.

Rather coarse, annual (?) herbs. Stems 0.5–1 m. tall and to 1 cm. in diameter, erect, green above and gray-brown below, terete. Leaves membranaceous, the lateral veins prominent; the principal foliage leaves sessile, 3.0–13.3 cm. long and 1.2–4.5 cm. broad, oblong-lanceolate to lanceolate or more rarely elliptic, gradually acuminate at the apex, the base rounded or truncate, more or less auriculate, clasping; upper leaves and those on the secondary branches smaller, lanceolate or ovate-lanceolate, rounded or cuneate at the base, subsessile or short-petiolate, not clasping.

Inflorescences of pedunculate dichasia, these typically once-compound, but rarely 2–4 times compound, and then the lateral branches often scorpioid, or occasionally apparently simple; inflorescence branches terete or indistinctly angled. Flowers nodding, the pedicels relatively stout, 3–10 mm. long; bracteoles subulate, scarious. Calyx 6–11.5 mm. long, fused for 1/8–1/5 its length; the lobes 5–10 mm. long and 1.5–2.5 mm. broad. lanceolate, acuminate, scarious-margined, ridged abaxially; the tube 1–1.5 mm. long. Corolla 2.7–4.0 cm. long, tubular-funnelform, uniformly bright yellow; the tube 2.2–3.1 cm. long and 4–6 mm. in diameter at the apex; the lobes 5.5–9 mm. long and 2–3 mm. broad, 2/10–3/10 as long as the tube, spreading, ovate-lanceolate, short-acuminate. Stamens inserted on the corolla tube ca. 1/3 of the distance from the base to the apex; filaments 1.5–2.7 cm. long, exceeding the corolla tube, the longest ones usually equalling or nearly equalling the style; anthers 1–2 mm. long and 1–1.5 mm. broad, broadly oblong, almost square, truncated at the apex. Ovary ovoid; style 1.8–3.0 cm. long, surpassing the corolla tube; stigma peltate. Capsule ovoid, usually broadly so, short-beaked, 5–11 mm. long, not including the 1 mm. long beak, and 3–6 mm. in diameter; calyx in fruit usually equalling or surpassing the capsule, rarely only 2/3 as long; marcescent corolla usually but not always persisting until the seeds are shed. FLOWERING: Jan.–Oct.

DISTRIBUTION: On limestone or other soils, in pinelands, grassy slopes, or on cliff faces in western Cuba (Pinar del Rio) (MAP 8).

REPRESENTATIVE COLLECTIONS

Cuba: without exact locality, *Wright s.n.* (GH; possibly an isotype). PINAR DEL RIO: Bahia Honda, Loma de Cajálbana, *Ekman 12722* (S); pinelands, Cajálbana, *Alain & Acuña 1106* (NY, US); base of Sierra Guane, *Shafer 10548* (NY); San José de Sagua to San Marcos, *Shafer 11967* (NY, US); vicinity of Sumidero, *Shafer 13389* (BM, F, US, NY); Loma Pelada de Buenavista, Cayajabos, *León 13204* (GH); Sierra de los Organos, hills around Arr. Rosario, W. of Cayajabos, *Ekman 12970* (S).

Lisianthius silenifolius is the only member of subsect. HERBACEI found in the Greater Antilles. It is easily distinguishable from *L. glandulosus* (sect. LISIANTHIUS subsect. FRUCTICOSI), the only other Cuban species, by its sessile, clasping leaves, its terminal inflorescences, and its ovoid capsules. In addition, *L. silenifolius* is restricted to Pinar del Rio Province in western Cuba, while *L. glandulosus* is found only in Oriente Province on the eastern end of the island.

No unquestionably authentic material of *Lisianthius silenifolius* has been seen. However, the characters described in the original diagnosis leave no doubt as to the plant Grisebach had at hand. In addition, no other species is found in western Cuba. A Wright specimen of *L. silenifolius*, collected between 1860 and 1864, is present in the collections at the Gray Herbarium. This specimen, which I have seen, is a possible isotype.

7. **Lisianthius quichensis** Donn. Sm. Bot. Gaz. **52**: 51. 1911 (as *Lisianthus*). TYPE. **Guatemala.** QUICHÉ: Río Negro, *Heyde & Lux 2921* (US!).

Coarse, perennial herbs. Stems 0.8–2 m. tall and to 1 cm. in diameter, erect or ascending, green, terete or nearly so. Leaves firmly membranaceous, the lateral veins prominent; principal foliage leaves sessile, (4.2) 6.8–21.5(24) cm. long and (1.2)2.0–5.7 cm. broad, broadest at or above the middle, narrowly elliptic or somewhat oblanceolate, long-attenuate and narrow at the base; upper leaves and those on the secondary branches smaller, 1.2–10.5 cm. long and (0.6)1.5–3.3 cm. broad, lanceolate, cuneate, short-petiolate. Inflorescences of long-pedunculate dichasia, these 1 to 3 times compound and the lateral branches often scorpioid, or occasionally appearing simple; inflorescence branches terete, elongate and the inflorescences loose and open. Flowers nodding or horizontal, the pedicels 2–13 mm. long; bracteoles subulate, scarious. Calyx (6)7.5–13 mm. long, fused for ca. 1/5 of its length; the lobes (4.5)6–11 mm. long and 1.5–2.5 mm. broad, lanceolate or subulate-lanceolate, long-acuminate, scarious-margined, ridged or indistinctly carinate; the tube 1.5–3 mm. long. Corolla (2.6)3–4.2 cm. long, tubular, uniformly yellow; the tube (2.3)2.7–3.5 cm. long and 3–7 mm. in diameter at the broadest point, somewhat inflated in the midparts and constricted slightly at the apex; the lobes 3–6(8) mm. long and 1.5–3 mm. broad, more than 2-times as long as broad, 1/8–1/4 as long as the tube, erect, not at all spreading, ovate-lanceolate to almost triangular, gradually acuminate. Stamens inserted on the corolla tube 1/3–2/5 of the distance from the base to the apex; filaments 1.8–3.4 cm. long, at least the longest and frequently all exceeding the corolla lobes, the longest one usually equalling or slightly exceeding the style; anthers 1.5–2.5 mm. long and 1–1.5 mm. broad, oblong, truncate or rounded at the apex, the connective sometimes very slightly exserted. Ovary ovoid; style 2.1–4 cm. long, always surpassing the corolla lobes, often conspicuously; stigma peltate. Capsule broadly ovoid, 6–12 mm. long and 3.5–6 mm. broad; calyx in fruit equalling or surpassing the capsule; the marcescent corolla persisting until long after the seeds are shed. FLOWERING: Mar.–Sept. CHROMOSOME NUMBER: $n = 18$.

DISTRIBUTION: From 900 to 1600 meters on open, rocky slopes, in secondary scrub, and on roadside banks in eastern Chiapas, Mexico, and north central Guatemala (MAP 3).

REPRESENTATIVE COLLECTIONS

Mexico. CHIAPAS: Los Lagos, 3 mi. nw. of Rancho San José (34 mi. se. of Comitán), s. shore of Lake Montebello, *Carlson 1835* (F, MICH, US); La Trinitaria at Lake Tsikaw on the Guatemalan border, 30 mi. e. of La Trinitaria, *Breedlove 10062* (DS, DUKE, F); Ocosingo, near Laguna Ocotal Grande, ca. 25–30 km. se. of Monte Líbano, *Dressler 1626* (BM, F, GH, MEXU, MICH, NY, UC, US); San Carlos á Santa Rita, *Miranda 7130 bis* (MEXU). **Guatemala:** ALTA VERAPAZ: along Quiché Highway about 12 km. w. of San Cristóbal, *Standley 89711* (F); 7 mi. w. of San Cristóbal Verapaz on Highway 7W, *Weaver*

2177 (A, BM, DUKE, F, LL, MICH, MO, NY, US); 3.5 mi. w. of San Cristóbal Verapaz on Highway 7W, *Weaver 2178* (A, BM, DS, DUKE, F, IJ, LL, MICH, MO, NY, S, UC, US). HUEHUETENANGO: between Las Palmas and Chaculá, Sierra de los Cuchumatánes, *Steyermark 51743* (F); vicinity of Maxbal, ca. 17 mi. n. of Barillas, Sierra de los Cuchumatánes, *Steyermark 48695* (F). QUICHÉ: Río Negro, *Heyde & Lux 2921* (GH, MO, NY, US; isotypes).

Lisianthius quichensis is a rather uncommon plant and until recently has been infrequently collected. Its closest relatives are probably *L. nigrescens* and *L. oreopolus*. It differs from both of these species by having leaves which are narrowed at the base and not clasping. It differs further from *L. nigrescens* in its yellow corollas, inflated corolla tube, and generally shorter corolla lobes. From *L. oreopolus*, *L. quichensis* differs also in its much shorter, erect corolla lobes.

Lisianthius quichensis has frequently been confused with *L. saponarioides* Cham. & Schlecht., a very dissimilar plant. Perkins (1902) referred to *L. saponarioides* the collection (*Heyde & Lux 2921*) later designated as the type of *L. quichensis*, a fact noted by Williams (1969), and discussed in this treatment under *L. saponarioides*.

8. **Lisianthius brevidentatus** (Hemsl.) O. Ktze. Rev. Gen. Pl. 2: 429. 1891.

Coarse, perennial herbs. Stems 0.5–1.5 m. tall and to 1 cm. in diameter, terete below but 3–4-angled or -winged above, green. Leaves sessile, clasping, 3.2–20.4 cm. long and 1.2–5.1 cm. broad, the principal foliage leaves narrowly oblong-elliptic with a tendency to be widest slightly above the middle, broadly attenuate at the base, the apices acuminate or cuspidate-acuminate, the upper leaves and those on the lateral branches lanceolate to ovate or more rarely elliptic, rounded or subcordate at the base, sessile but not clasping, or short petiolate. Inflorescences usually of dichasia, these 1–4 times compound, borne singly or in groups of 3 or more rarely 5, with the terminal one often sessile or nearly so and the whole unit appearing pleiochasial, the ultimate branches monochasial and resembling secund racemes; inflorescence branches short and the dichasia or groups of dichasia consequently dense and compact, or elongate and the dichasia loose and open, terete or indistinctly angled or more commonly 2–3-winged, if 3-winged, 2 of the wings decidedly broader than the third, the wings to 1 mm. broad. Flowers sessile or the pedicels to 3 mm. long, the bracteoles scarious, subulate, 1–3 mm. long and 0.5–1 mm. broad. Calyx 6–9.5 mm. long, fused for 1/5–1/3 its length; the lobes 4.5–6 mm. long and 1–2 mm. broad, lanceolate, long acuminate, ridged abaxially, scarious-margined; the tube 1.5–3 mm. long. Corolla tubular, somewhat fleshy, 2.4–3.4 cm. long; the tube yellow, 2.2–3.0 cm. long and 3–4 mm. broad, conspicuously white-striate at base, especially with age; the lobes 2–4 mm. long and 2–3 mm. broad, greenish-yellow, spreading or slightly recurved at the apex, squarish to suborbicular or ovate, abruptly short-acuminate, auriculate at the base or not. Stamens

inserted on the corolla tube just below the middle, well above the apex of the calyx lobes; filaments 1.4–1.7 cm. long, equalling or barely exceeding the corolla tube; anthers 2–3.5 mm. long and ca. 1 mm. broad, narrowly oblong, 2–3 times as long as broad. Style 2.3–3.3 cm. long, surpassing the corolla lobes in mature flowers, always exceeding the stamens in relative position; stigma peltate. Capsule oblong-ellipsoid, 8–13 mm. long and 3–5 mm. in diameter; the persistent calyx 2/3 to nearly as long as the capsule; the marcescent corolla strongly persisting.

KEY TO THE VARIETIES

Inflorescence branches contracted and the dichasia or groups of dichasia appearing dense and compact; corolla lobes squarish to suborbicular, about as broad as long, auriculate at the base; calyx fused for 1/4–1/3 its length. . . . . a. var. *brevidentatus*.

Inflorescence branches elongate and the dichasia or groups of dichasia appearing loose and open; corolla lobes ovate, longer than broad, not auriculate at the base; calyx fused for ca. 1/5 its length. . . . . b. var. *collinus*.

8a. Lisianthius brevidentatus (Hemsl.) O. Ktze. var. brevidentatus.

Leianthus brevidentatus Hemsl. Biol. Centr. Am. Bot. 2: 344. 1882. TYPE. **Guatemala:** Sierra del Mico, *Bernoulli 942*, photograph (DUKE!), holotype (K).

Lisianthus elatus Standl. & Steyerm. Fieldiana Bot. 22: 267, 268. 1940. TYPE. **Guatemala.** IZABAL: between milla 49.5 and ridge 6 mi. from Izabal, Montaña del Mico, *Steyermark 38562* (F!).

Inflorescence branches contracted and the dichasia or groups of dichasia dense and compact. Calyx 6–9.5 mm. long, fused for 1/4–1/3 its length, the lobes 4.5–6 mm. long and 1–2 mm. broad, the tube 1.5–3 mm. long. Corolla lobes squarish to suborbicular, about as broad as long, 2–3 mm. long and 2–3 mm. broad, auriculate at the base. FLOWERING: Feb.–Aug. CHROMOSOME NUMBER: $n = 18$.

DISTRIBUTION: In pine forests, open rocky slopes, and along roadsides from near sea level to 1000 meters in the Departments of Alta Verapaz and Izabal, Guatemala (MAP 3).

SPECIMENS EXAMINED

Guatemala. ALTA VERAPAZ: on Guat. 4, 45 km. ne. of Cobán. *Stone 2765* (A, BM, DS, DUKE, F, IJ, LL, MICH, MO, NY, S, UC, US); vicinity of caves, sw. of Lanquín, *Steyermark 44140* (F, US); sobre el paredón del camino entre San Pedro Carchá y Sacouyou, *Molina & Molina 12115* (F). IZABAL: 0.8 mi. from Highway CA–9 on road to Mariscos, *Weaver 2184* (A, BM, DUKE, F, LL, MICH, MO, S, US); along Highway CA–9 near turnoff to Mariscos, *Weaver 2186* (A, DUKE, F, MICH, US); trail from Los Amates to Izabal, *Blake 7795* (GH, US); Sierra del Mico, *Bernoulli 924* (NY, isotype); between milla 49.5 and ridge 6 mi. from Izabal, *Steyermark 38562* (F; type of *L. elatus*).

8b. **Lisianthius brevidentatus** (Hemsl.) O. Ktze. var. **collinus** (Standl.) Weaver, comb. nov.

Lisianthus collinus Standl. Carnegie Inst. Publ. **461**: 81. 1935. TYPE. **British Honduras:** Jacinto Hills, *Schipp 1205* (F!).

Inflorescence branches elongate and the dichasia or groups of dichasia appearing loose and open. Calyx 6.5–7.5 mm. long, fused for ca. 1/4–1/3 its length, the lobes 5–6 mm. long and 1–1.5 mm. broad, the tube ca. 1.5 mm. long. Corolla lobes ovate, 2/3 mm. broad.

DISTRIBUTION: Known only from the type locality on a cliff face in peaty soil at 300 ft. elevation (MAP 3).

SPECIMENS EXAMINED

British Honduras. TOLEDO (?) DIST: Jacinto Hills, *Schipp 1205* (GH, MICH, MO, S, UC, isotypes).

Williams (1968, 1969) included under *Lisianthius brevidentatus* a rather diverse assemblage of plants, including, as I have interpreted them, *L. quichensis* Donn. Sm., *L. calciphilus* Standl. & Steyerm., and a hybrid between *L. axillaris* and *L. saponarioides* (previously known as *L. petenensis* Standl. & Steyerm.). Williams (1968, p. 407) did note that there are differences, in the inflorescence, calyx, and corolla, in the material he placed under *L. brevidentatus*. He remarked, however, that these differences are ones which may depend on the stage of growth of the plants, or that they are not easily defined. The following table compares Williams's treatment and mine of the same plants.

WILLIAMS (1968, 1969)	WEAVER
L. brevidentatus (Hemsl.) O. Ktze.	*L. brevidentatus* (Hemsl.) O. Ktze. var. *brevidentatus*
(*L. elatus* Standl. & Steyerm.)	(*L. elatus* Standl. & Steyerm.)
(*L. collinus* Standl.)	*L. brevidentatus* var. *collinus* (Standl.) Weaver
(*L. quichensis* Donn. Sm.)	*L. quichensis* Donn. Sm.
(*L. calciphilus* Standl. & Steyerm.)	*L. calciphilus* Standl. & Steyerm. (*species non satis nota*)
(*L. petenensis* Standl. & Steyerm.)	A hybrid (no formal designation)

Lisianthius quichensis, the range of which closely approaches that of *L. brevidentatus* in central Guatemala, is rather easily distinguished from that species. *L. quichensis* differs by corolla lobes 3–8 mm. long, more than twice as long as broad, and long-acuminate; the corolla tube distinctly inflated in the middle; flowers distinctly pedicellate; inflorescence branches angled but not winged; dichasia never sessile and the dichasial groups never appearing pleiochasial; capsules broadly ovoid; and the

filaments, at least the longer ones, exceeding the corolla lobes; and leaves narrowed at the base and not clasping.

Lisianthius calciphilus, which is known from a single specimen from Dept. Alta Verapaz, Guatemala, also differs strikingly from *L. brevidentatus* in a number of characters: much longer corolla lobes, nearly twice as long as broad, gradually short acuminate; the corolla distinctly funnelform; the flowers distinctly pedicellate; and the bracteoles conspicuous, oblanceolate, to 8 mm. long, and green at least in part. This plant is here treated as a *species non satis nota*.

Lisianthius elatus Standl. & Steyerm., known only from the holotype, *Steyermark 38562* (F) from Dept. Izabal, Guatemala, is synonymous with *L. brevidentatus*. With the original description of *L. elatus*, Standley and Steyermark speculate that the most closely related species is *L. collinus* Standl. and note that *L. collinus* differs in having "a lax inflorescence with scattered flowers, some of which are borne on greatly elongate pedicels" (measurements of all available specimens of *L. collinus*, however, show that the pedicels are never more than 3 mm. long, hardly elongate).

The holotype of *Lisianthius brevidentatus*, *Bernoulli 924* (K) from the Sierra del Mico, Guatemala, was not available for study, but I have seen a photograph of it. There is a specimen of *Bernoulli 924* at the New York Botanical Garden, and it undoubtedly represents the same taxon as the holotype. Therefore I have used this specimen as typical of *L. brevidentatus* for comparison with *L. elatus*. Even a cursory examination leaves no doubt that the holotype of *L. elatus* is an entirely typical specimen of *L. brevidentatus* var. *brevidentatus*.

Actually, it is possible that at the time they described *L. elatus*, Standley and Steyermark were unfamiliar with typical *L. brevidentatus*. Indeed in 1940 there were no more than three specimens of *L. brevidentatus* in American herbaria, and none were at the Field Museum.

Lisianthius collinus Standl. is known from a single collection, *Schipp 1205*, from the Jacinto Hills in southern British Honduras. These specimens resemble *L. brevidentatus* in all respects except that the inflorescences are loose and open and the corolla lobes are slightly longer in relation to their width, distinctly ovate, and without auricles at the base. Standley, in describing it, compared *L. collinus* only with *L. axillaris*. However, it is undoubtedly closely related to *L. brevidentatus*, but certainly distinct. In view of its apparent distinctness and the fact that typical *L. brevidentatus* is absent from British Honduras, but with an eye to caution because of the extremely limited number of specimens available, I prefer to treat *L. collinus* as a variety of *L. brevidentatus*, rather than to submerge it entirely as did Williams or to treat it as a distinct species as did Standley. Perhaps more adequate collections will necessitate a change in its status.

9. **Lisianthius viscidiflorus** Robins. Proc. Am. Acad. **45**: 398. 1910 (as *Lisianthus*). TYPE. **Guatemala.** ALTA VERAPAZ: Cobán, *von Tuerckheim II–1308* (GH!).

Coarse, perennial herbs. Stems 0.5–2.5 m. tall and to 1.5 cm. in diameter, erect, green and terete above, gray-brown and somewhat quadrate below. Leaves firmly membranaceous, sessile, clasping, (3.1)4.9–18 cm. long and 1.3–7.2 cm. broad, oblong, oblong-elliptic, or tending toward oblanceolate, more rarely ovate, the apices short-acuminate, the bases broadly rounded or subcordate or rarely narrow and tapering; upper leaves and those on the lateral branches smaller, 1.3–7.2 cm. long and 0.3–2.5 cm. broad, narrowly ovate or lanceolate. Inflorescences of long-pedunculate dichasia, these 1–5 times compound or apparently simple, the lateral branches often scorpioid and secund. Flowers horizontal, weakly ascending or weakly nodding, the pedicels stout, 2–14(21) mm. long; bracteoles scarious, subulate. Calyx 4.5–8 mm. long, fused for 1/3–1/2 its length; the lobes 1.5–5 mm. long and 1.5–2.5 mm. broad, narrowly ovate to lanceolate and ovate, short-acuminate or more rarely acute, becoming somewhat blunt with age, scarious-margined, completely ecarinate; the tube 1.5–4 mm. long. Corolla tubular, glutinous, 2.9–3.9 cm. long; the tube 1.9–3.4 cm. long and 4–5 mm. in diameter at the apex, dull red; the lobes 3.5–5.5 mm. long and 2–3.5 mm. broad, 1/8–1/6 as long as the tube, spreading, greenish with a dull purple base, narrowly ovate, the apex blunt and somewhat undulate and erose, very rarely the apex acute. Stamens inserted on the corolla tube 1/3–2/5 of the distance from the base to the apex; filaments 1.5–2.9 cm. long, the shortest sometimes barely surpassing the corolla tube, the longest ones always surpassing the corolla lobes in mature flowers and frequently equalling or exceeding the style; anthers 2–3 mm. long and 1–1.5 mm. broad, oblong, the apex truncate or retuse. Style 1.8–3.4 cm. long, always exceeding the corolla lobes in mature flowers; stigma peltate. Capsule narrowly ovoid or oblong-ellipsoid, lustrous, glutinous, short-beaked, 9–14 mm. long, not including the 1–2 mm. long beak, and 3–6 mm. in diameter; calyx in fruit 1/3–2/5(1/2) as long as the capsule; the marcescent corolla not persisting until the seeds are shed. FLOWERING: Mar.–Sept. CHROMOSOME NUMBER: $n = 18$.

DISTRIBUTION: From 150–1300 meters, along roadsides and in secondary scrub in central Guatemala and Chiapas, Mexico (MAP 4).

SPECIMENS EXAMINED

Mexico. CHIAPAS: Laguna Ocotal Grande, ca. 25–30 km. se. of Cerro Líbano, *Dressler 1448* (MEXU, MICH, NY, US). **Guatemala.** ALTA VERAPAZ: 3.5 mi. w. of San Cristóbal Verapaz on Highway 7W, *Weaver 2179* (A, DUKE); Cobán, *Johnson 718* (F, US); 1.5–2 mi. s. of Gubilguitz, *Steyermark 44431* (F, NY, US); Cobán Road, between km. 284–285, between Chiracté and Chapultepec Farm, *Contreras 4725* (LL); along road, between San Cristóbal Verapaz and Chixoy, *Steyermark 43885* (F); Cerro Chinajá, between Finca Yalpemech and Chinajá, above source of Río San Diego, *Steyermark 45672* (F); Cóban, *von Tuerckheim 1308* (F, MO, US; isotypes). QUICHÉ: 24.1 mi. e. of Cunén on Highway 7W, *Weaver 2182* (A, BM, DS, DUKE, F, IJ, LL, MICH, MO, NY, S, UC, US).

Although *Lisianthius viscidiflorus* is a rather poorly collected species,

it is quite common along roadsides in the vicinity of Cobán, Dept. Alta Verapaz, Guatemala. The flowers are predominantly red but the plant is not particularly conspicuous even when in full flower. *L. viscidiflorus* is unique in the genus in having mostly obtuse corolla lobes and purple anthers. It is easily distinguishable by these characters and the red corolla tube from the other species of sect. LISIANTHIUS subsect. HERBACEI. Of these species it most closely resembles *L. brevidentatus* in corolla and leaf form. *L. axillaris* (sect. LISIANTHIUS subsect. FRUTICOSI), the only other species in the genus with red corolla tubes, differs strongly from *L. viscidiflorus* in having acuminate corolla lobes, yellow anthers, and solitary axillary flowers.

As the specific epithet implies, and as pointed out by Robinson in the original description, the flowers of *Lisianthius viscidiflorus* are sticky, both in the fresh state and during the drying process. *L. viscidiflorus*, however, is not unique in this respect. The corolla of several species, particularly *L. longifolius*, and the young buds and capsules of most of the species are viscid to some degree.

Lisianthius viscidiflorus is a very distinct species, not particularly variable in most of its characters. However, the single known population from Chiapas, Mexico (*Dressler 1448*), differs from the Guatemalan populations in having acute rather than obtuse corolla lobes. This is the only consistent difference between the populations and is, I think, not of sufficient magnitude to warrant the recognition of the two as formal varieties.

Lisianthius sect. **Lisianthius** subsect. **Fruticosi** Weaver, subsect. nov.

Suffrutices, frutices vel arbores graciles, glabrae vel puberulae. Plantae ramosae, ramis indeterminatis. Folia petiolata vel raro subsessilia. Inflorescentiae axillares vel in ramulis determinatis dispositis, raro flores solitarii, axillares. Capsulae oblongo ellipsoideae. SPECIES TYPICA: *L. longifolius* L.

KEY TO THE SERIES

A. Inflorescences not densely compacted, obviously dichasioid, or reduced to single flowers and subtended by foliaceous or scarious bracts, but these not involucrate.
  B. Filaments and styles shortly exserted, the exserted portion much less than the total length of the corolla; pollen grains reticulate. . . . . a. *Longifolii.*
  B. Filaments and styles greatly exserted, the exserted portion at least equal to the total length of the corolla; pollen grains appearing smooth or nearly so with the light microscope. . . . . b. *Exserti.*
A. Inflorescences densely compacted, appearing umbellate or capitate and subtended by 2 pairs of foliaceous involucral bracts. . . . . c. *Umbellati.*

a. **Lisianthius** sect. **Lisianthius** subsect. **Fruticosi** ser. **Longifolii** Weaver, ser. nov.

Suffrutices vel frutices, omnino glabri vel puberuli. Inflorescentiae dichasiales, diffusae, bracteis foliaceis vel scariosis non involucratis subtentae, ramulis elongatis, flores raro solitarii. Lobi calycis saepe carinati vel alati. Styli filamentaque breviter exserta. Pollinis grana exinio reticulato. SPECIES TYPICA: *L. longifolius* L.

With its 15 species, series *Longifolii* is the largest species group in the genus. Seven of the species are distributed in Mexico and Central America, with one species ranging barely into northwestern Colombia. The remainder are distributed throughout the Greater Antilles, with a majority in Jamaica (five species) and one species on each of the other three islands. The group is rather diverse morphologically, but all of the species are shrubs or subshrubs with inflorescences arranged diffusely on determinate, lateral flowering branches or rarely reduced to solitary, axillary flowers.

KEY TO THE SPECIES OF SERIES LONGIFOLII

A. Corolla tube red; flowers typically borne singly in the axils of the foliage leaves. ..... 21. *L. axillaris.*

A. Corolla tube yellow; flowers borne in dichasia, these axillary or on determinate, lateral flowering branches, very rarely the flowers borne singly in the axils of the foliage leaves.

B. Corolla tube distinctly inflated, widest above the middle but constricted at the apex; corolla lobes and the apex of the tube often dark green; leaves coriaceous or membranaceous, broadest at or above the middle.

C. Corolla lobes 1.2–2.0 cm. long, ca. 1/2 as long as the tube; leaves coriaceous; corolla lobes greenish-yellow; calyx lobes completely ecarinate; corolla strongly persistent on the mature capsules; plants of Jamaica. ..... 13. *L. adamsii.*

C. Corolla lobes 1 cm. or less in length, less than 1/4 as long as the tube; leaves coriaceous or membranaceous; corolla lobes greenish-yellow or dark green; calyx lobes carinate or at least ridged abaxially; corolla not persisting on the mature capsules; plants of Central America.

D. Stamens inserted well above the apex of the calyx lobes; calyx in fruit 1/5–2/5 as long as the capsule; corolla lobes less than 2 times as long as broad, usually less than 1/8 as long as the tube; calyx 5–8 mm. long, the lobes narrowly ovate and abruptly short-acuminate, more rarely ovate-lanceolate and longer acuminate. ..... 10. *L. skinneri.*

D. Stamens inserted at or just above the apex of the calyx lobes; calyx in fruit 1/2 as long to nearly as long as the capsule; corolla lobes 2 times as long as broad or longer, more than 1/6 as long as the tube; calyx 7–13.5 mm. long, the lobes lanceolate and long-acuminate.

E. Leaves membranaceous; corolla (4.2)4.7–5.9 cm. long, the lobes 7–10 mm. long, the tube 4–5 times as long as the calyx; styles barely surpassing the corolla lobes, the filaments never surpassing the corolla lobes. ..... 11. *L. peduncularis.*

E. Leaves more or less coriaceous; corolla 2.5–4.2 cm. long,

the lobes 4–6.5 mm. long, the tube less than 4 times as long as the calyx; the longer filaments and the styles surpassing the corolla lobes, the latter conspicuously so. . . . . 12. *L. jefensis.*

B. Corolla tube not inflated, widest at the apex; corolla lobes yellow or greenish-yellow; leaves membranaceous or very rarely coriaceous, usually broadest at or below the middle.

F. Plants glabrous, or very rarely minutely spiculate; calyx lobes never alate; flowering branches very rarely with leaves above the first division and never on the secondary axes; corolla seldom persisting until the seeds are shed.

G. Inflorescences congested, of compound dichasia, the lateral branches scorpioid or helicoid; corolla paler inside than out; flowering branches with 3 to many pairs of leaves below the lowermost division. . . . . 22. *L. seemannii.*

G. Inflorescences diffuse, mostly of apparently simple dichasia, the lateral branches not scorpioid or helicoid; corolla the same color inside as out; flowering branches rarely with more than 1 pair, and never more than 3 pairs of leaves below the lowermost division.

H. Filaments, at least the longest ones in each flower, exceeding the corolla lobes.

I. Corolla lobes ca. 1/2 as long as the tube, and acute or abruptly short-acuminate; leaves usually broadest above the middle, gray-green, thick and somewhat coriaceous, the lateral veins indistinct; plants of Jamaica. . . . . 13. *L. adamsii.*

I. Corolla lobes less than 1/3 as long as the tube and long cuspidate-acuminate; leaves broadest at or below the middle, green, thin-membranaceous, the lateral veins prominent; plants of Central America. . . . . 15. *L. auratus.*

H. Filaments not exceeding the corolla lobes.

J. Corolla lobes 5–6 times as long as broad, more than 3/5 as long as the tube and gradually long-acuminate; calyx ca. 1/2 as long as the corolla tube. . . . . 18. *L. laxiflorus.*

J. Corolla lobes less than 4 times as long as broad, 1/2 or less as long as the tube, acute or abruptly short-acuminate, very rarely gradually acuminate; calyx 1/3 or less as long as the corolla tube.

K. Corolla lobes less than 1/3 as long as the tube.

L. Styles surpassing the corolla lobes in mature flowers; bracteoles below the pedicels green, at least along the midline; flowers ascending; calyx fused for 2/10–1/3 its length; stigma peltate; filaments 2.1–2.7 cm. long, inserted on the corolla tube ca. 1/3 of the distance from the base to the apex; plants of Mexico. . . . . 14. *L. acuminatus.*

L. Styles not surpassing the corolla lobes in mature flowers; bracteoles below the pedicels scarious;

flowers horizontal or nodding; calyx fused for 1/10–2/10 its length, stigma capitate; filaments 1.0–2.2 cm. long, inserted on the corolla tube just below the middle; plants of Cuba. ..... 17. *L. glandulosus.*

K. Corolla lobes more than 1/3 as long as the tube.

M. Inflorescence branches terete or indistinctly angled, the angles never expanded into narrow, scarious wings; dichasia, at least the terminal ones, 2–3-flowered; leaves more than 2.5 times as long as broad, long-petiolate; plants of Jamaica.

N. Corolla tube tightly constricted in the lower third, then expanding abruptly; styles nearly always surpassing the corolla lobes; capsule short-beaked, the beak less than 1/4 as long as the capsule. ..... 16. *L. troyanus.*

N. Corolla tube more or less gradually expanding from the base; styles never surpassing the corolla lobes; capsule long-beaked, the beak 1/3–1/2 as long as the capsule. ..... 19. *L. latifolius.*

M. Inflorescence branches strongly angled, the angles often expanded into narrow, scarious wings; dichasia reduced to 1 or rarely 2 flowers; bracteoles below the pedicels green; leaves less than 2.5 times as long as broad, subsessile or petiolate; plants of Hispaniola. ..... 20. *L. domingensis.*

F. Plants, especially the inflorescence, puberulous, if nearly glabrous, the calyx lobes broadly alate abaxially; flowering branches with leaves above the first division and often on the secondary axes; corolla persisting long after the seeds are shed.

O. Calyx lobes alate or very rarely merely carinate; leaves on the flowering branches obtuse or rounded or very rarely subcordate at the base; branching opposite or alternate below and usually opposite above; inflorescences, especially those at the apex of the flowering branches, 2–3-flowered. ..... 23. *L. longifolius.*

O. Calyx lobes carinate abaxially; leaves on the flowering branches, at least the upper ones, distinctly cordate at the base; branching alternate or bifurcate, very rarely opposite; inflorescences 2-flowered or the flowers solitary. ..... 24. *L. cordifolius.*

10. **Lisianthius skinneri** (Hemsl.) O. Ktze. Rev. Gen. Pl. 2: 429. 1891 (as *Skinneri*).

Leianthus skinneri Hemsl. Biol. Centr. Am. Bot. 2: 345. 1882. LECTOTYPE. **Guatemala:** without exact locality, *Skinner* (K); photo. (MO!).

Lisianthus arcuatus Perk. Bot. Jahrb. 31: 492. 1902. TYPE. None designated; *Warscewicz 9* (Costa Rica et Veragua) and *Hoffmann 832* (Desengano) cited, both presumably at Berlin and destroyed during World War II.

Lisianthus scopulinus Robyns & Elias, Ann. Mo. Bot. Gard. 55: 62. 1968.

TYPE. **Panama.** VERAGUAS: Mouth of the Río Concepción, *Lewis, Croat & Hawker 2799* (MO).

Shrubs or more rarely subshrubs, glabrous throughout. Stems 0.5–3 m. tall and to 2 cm. in diameter, erect or ascending, rarely sprawling, gray-brown below and green above, terete. Leaves membranaceous, glossy, dark or rather pale green above and distinctly paler beneath, the blades 3.5–20(24.5) cm. long and 1.5–5.5(7.7) cm. broad, narrowly elliptic to narrowly obovate (broadly elliptic), generally widest above the middle, abruptly acuminate, the bases long-attenuate into the winged petiole; the upper leaves essentially sessile or the petioles to 2 cm. long. Inflorescences of pedunculate, apparently simple (1-compound or rarely 3-compound) dichasia, occasionally reduced to 1 or 2 flowers; flowering branches ascending, usually ternately divided, each division terminated by a dichasium or group of dichasia; axes of the flowering branches and the dichasial branches indistinctly 4-angled to essentially terete, elongate and the inflorescences appearing loose and open. Flowers horizontal or nodding, the pedicels 0.7–2.4 cm. long; bracteoles subulate, scarious. Calyx 4.5–8 mm. long, united for 3/10–3/5 of its length, 1/10–1/6(1/5) as long as the corolla tube; the lobes 2–5 mm. long and 1.5–3 mm. broad, narrowly ovate (lanceolate, broadly ovate, or suborbicular), abruptly short-acuminate (long-acuminate or acute), scarious-margined, ridged or carinate abaxially; tube 1.5–3.5 mm. long. Corolla tubular, more or less fleshy or thinner, 2.7–6.3 cm. long; tube 2.4–5.7 cm. long and 0.4–1.1 cm. broad at the widest point, bright yellow but with a green or yellow-green apex, constricted in the lower 1/4–1/3, inflated in the mid-portions; lobes 2.5–6 mm. long and 2.5–4 mm. broad, (1/6)1/8–1/12 as long as the tube, yellowish-green, or rather dark green with yellow green margins, spreading and with the tips often recurved, triangular-ovate and abruptly short-acuminate (ovate-lanceolate and rather long-acuminate). Stamens inserted in the lower third of the corolla tube; filaments 2–5 cm. long, at least the longest ones equalling or surpassing the corolla lobes, the longest ones sometimes surpassing the style; anthers 1.5–3.5 mm. long and 1–1.5 mm. broad, broadly oblong, the connective slightly exserted. Style 2.3–5.3 cm. long, exserted, usually surpassing the corolla lobes; stigma peltate. Capsules narrowly oblong-ellipsoid, conspicuously beaked, 1–2.2 cm. long, not including the 1–6 mm. long beak, and 4–6 mm. in diameter; the marcescent corolla falling off before the seeds are shed. FLOWERING: Jan.–Sept. CHROMOSOME NUMBER: $n = 18$.

DISTRIBUTION: From sea level to 1300 meters in moist forests, generally along the edge, or along roadsides, on the Atlantic Coastal Plain of southeastern Guatemala and adjacent Honduras and again in Panama, and at middle elevations in the interior of Costa Rica and Panama (MAP 4).

REPRESENTATIVE COLLECTIONS

Guatemala. IZABAL: south shore of Lake Izabal, west of the village of Izabal, *Proctor, Jones & Facey 3049* (F, IJ, LL, MEXU, US). **Honduras.** ATLANTIDA:

south of San Alejo near Río San Alejo, *Standley 7829* (F); Cuyamel, *Carleton 584* (F). **Costa Rica.** ALAJUELA: Villa Quesada, *Smith 1884* (F, MO, NY); Cataratas de San Ramón, *Brenes 13575* (F, NY); ca. 13.5 mi. e. of Arenal and 6.5 mi. w. of Fortuna, *Wilbur & Stone 10257* (A, BM, DUKE, DS, F, IJ, LL, MICH, MO, NY, S, UC, US). GUANACASTE: Tilarán, *Valerio 1151* (F). HEREDIA: Sarapiquí, Isla Bonita, *Pittier s.n.* (NY, US); Finca Hnos. Vargas, Puerto Viejo de Sarapiquí, *Jiménez 3577* (F). **Panama.** COCLÉ: vicinity of La Mesa, El Valle de Antón, *Allen 2369* (MO); Bismarck, above Penonomé, *Williams 613* (NY). COLON: roadsides 5–7 mi. se. of Portobello, *Weaver & Wilbur 2249* (A, BM, DS, DUKE, F, IJ, LL, MICH, MO, NY, S, UC, US); summit of Cerro Santa Rita, *Allen 5104* (BM, MO). PANAMA: slopes of Cerro Jefe, along road from Cerro Azul, well below the turnoff to La Eneida, *Weaver & Wilbur 2244* (A, BM, DS, DUKE, F, IJ, LL, MICH, MO, NY, S, UC, US); VERAGUAS: mouth of the Río Concepción, *Lewis, Croat & Hawker 2799* (DUKE; isotype of *L. scopulinus*). CANAL ZONE: forest along telephone cable trail between Splice S16 & S49, Río Indio, *Steyermark & Allen 17427* (BM, DS, MO, S); headwaters of Río Arenal, near IWTC pump, *Johnston 1502* (A, MO).

Lisianthius skinneri is the most widespread species, ranging from southeastern Guatemala to central Panama; with *L. jefensis* and *L. peduncularis* it forms a rather distinctive, closely interrelated species group. These three species differ from one another in the length of the calyx, the shape and length of the corolla lobes, and the ratio between the lengths of the corolla lobes and the corolla tube. The differences are not striking, especially in view of the variation within *L. skinneri*, but they are constant. The close sympatry of *L. skinneri* with both of the other species and the absence of intermediate forms supports the maintenance of all three as distinct.

Lisianthius skinneri is a rather variable species, but no population is sufficiently distinct to warrant recognition as a subspecies or variety. There is no perceptible pattern to the variation. The Guatemalan plants are characterized by long, narrow, thin-textured corollas; long-acuminate, relatively long and narrow calyx and corolla lobes; and styles usually longer than the filaments. *Wilbur & Stone 10257*, from Volcán Arenal, Costa Rica, is characterized by long, narrow, rather fleshy corollas; merely acute calyx lobes; broad and very short-acuminate corolla lobes; and styles shorter than the filaments in a given flower. Other specimens from Costa Rica and those from Honduras and the interior of Panama resemble the Guatemalan plants but have a broader corolla, with calyx and corolla lobes broader and shorter acuminate, and styles and stamens various. The plants from the Atlantic Coastal Plain of Panama have a short, rather slender, fleshy corolla; broad, short-acuminate calyx and corolla lobes; and the styles conspicuously longer than the filaments.

Although no original material has been seen and duplicates have not been located, according to the original description *L. arcuatus* Perk. differs from *L. skinneri* in having arcuate rather than straight corollas and subelongate rather than short internodes. Internode length, especially in shrubs, depends largely on environmental factors and has proved of minimal taxonomic utility in this genus. Many dried specimens of *L.*

skinneri are indeed characterized by having flowers with arcuate corollas. Actually the corollas appear merely swollen on one surface and would more correctly be termed "gibbous" rather than "arcuate." This condition is almost certainly an artifact resulting from pressing and drying. The corollas of *L. skinneri* are conspicuously inflated (evenly) in the mid-portions, and frequently press unevenly. I have collected plants of *L. skinneri* in Panama and have observed the corollas are not gibbous in the fresh state. However, when dry my specimens frequently did have apparently gibbous corollas. There seems to be no basis whatever for maintaining *L. arcuatus* as distinct.

Lisianthius scopulinus Robyns & Elias reputedly differs from *L. skinneri* in having narrowly ovate, long-acuminate, and longer calyx lobes. I have seen an isotype of *L. scopulinus*, and it strongly resembles typical *L. skinneri* except that the corolla lobes are generally longer than usual. The longest calyx lobes (5 mm.) are indeed longer than any seen in specimens of *L. skinneri*. However, the shorter lobes (4 mm.) on this specimen are no longer than those, for instance, on *Proctor, Jones & Facey 3049* (F, IJ, LL, MEXU, US), perfectly good *L. skinneri*, from Lake Izabal, Guatemala, geographically rather far removed from the type and only known locality of *L. scopulinus* at the mouth of the Río Concepción in Veraguas, Panama. In addition, *L. skinneri* is not infrequently characterized by having rather long-acuminate, narrowly ovate calyx lobes. Therefore, it seems that *L. scopulinus* does not really differ in any significant way from *L. skinneri*.

When Hemsley (1882) described *Leianthus skinneri*, he cited two specimens as representative of the new taxon: a Skinner specimen, without a collection number (Guatemala, without exact locality) and *Fendler 137* (Panama: Chagres), both in the herbarium at Kew. I have not seen either specimen, but I have seen good photographs of both. *Fendler 137* is only a scrap, consisting of a flowering branch with five flowers, while the Skinner specimen is much more complete, showing stems, leaves, flowers, and capsules. Since the Skinner specimen is far superior and the species was named for its collector, I designate it as the lectotype of *Leianthus skinneri* Hemsley.

11. **Lisianthius pedunculariS** L.O. Williams, Fieldiana Bot. 31: 408. 1968 (as *Lisianthus*). ✓TYPE. **Panama.** COCLÉ: El Valle de Antón, *Allen 3410* (MO!).

Slender shrubs or subshrubs, glabrous throughout. Stems 1–2.5 m. tall and to 2 cm. in diameter, erect or ascending, terete, gray-brown and woody below, green and herbaceous above. Leaves glossy grass-green above, paler and dull beneath, the lateral veins prominent, the blades (3.2)5.2–13.5(18.0) cm. long and (1.1)2.0–5.4(8.4) cm. broad, narrowly obovate or oblanceolate (elliptic), widest at or above the middle, abruptly short-acuminate (acute), the bases long-attenuate into the winged, 0.4–2.0(3.2) cm. long petiole. Inflorescences of pedunculate, apparently simple

(1-compound) dichasia, these sometimes reduced to 1 or 2 flowers; flowering branches often with several pairs of reduced leaves below the first division, once- or rarely twice-ternately divided, each division terminated by a dichasium; dichasial branches and stalks 4-angled, elongate and with the inflorescences loose and open. Flowers nodding, the pedicels 6–14 mm. long; bracteoles subulate, scarious. Calyx 8–13.5 mm. long, fused for 1/8–1/5(1/4) its length; the lobes 6.5–11.5 mm. long and 1–2.5 mm. broad, lanceolate, long-acuminate, scarious-margined, weakly carinate abaxially; the tube 1.5–3 mm. long. Corolla tubular (4.2)4.7–5.9 cm. long; the tube (3.4)4–4.9 cm. long and 5.5–9 mm. broad at the broadest point, bright yellow, constricted in the lower third, inflated in the midportions; the lobes (7)8–10 mm. long and 3–4 mm. broad, 1/5–1/4 as long as the tube, spreading and recurved at the tips, greenish-yellow or rather dark green, lanceolate or ovate-lanceolate, long-acuminate. Stamens inserted on the corolla tube ca. 1/4 of the distance from the base to the apex; filaments (2.9)3.5–4.2 cm. long, the shorter ones barely surpassing the corolla tube, the longest ones not surpassing the corolla lobes; anthers 2–3 mm. long and 1–1.5 mm. broad, yellow, narrowly oblong, acutish, the connective slightly exserted. Style (3.2)4.0–5.2 cm. long, usually slightly exceeding the corolla lobes, always surpassing the filaments; stigma peltate. Capsule fusiform, long-beaked, 1.1–1.6 cm. long, not including the 2–3.5 mm. long beak, and 4–5 mm. in diameter; the marcescent corolla not persisting until the seeds are shed. FLOWERING: Jan.–June. CHROMOSOME NUMBER: $n = 18$.

DISTRIBUTION: Along roadsides and in dense moist forests at 1000 meters, just north of El Valle de Antón in central Panama (MAP 5).

SPECIMENS EXAMINED

Panama. COCLÉ: El Valle de Antón, *Allen 3410* (BM, MO; isotypes); El Valle, north rim, *Allen 1793* (GH, MO, NY); inside the crater of El Valle de Antón at La Mesa, *Weaver, Wilbur & Correa 2247* (A, DUKE, F, LL, MICH, MO, NY, US).

Lisianthius peduncularis is known only from the type locality where it is a rather rare plant. Although the species was only described in 1968, specimens of *L. peduncularis* have been present in collections since 1939. All of the known specimens had been determined as "*L. latifolius* Sw.", a Jamaican species resembling *L. peduncularis* primarily in its large, broad leaves.

The affinities of *Lisianthius peduncularis* are clearly with *L. skinneri* and *L. jefensis*. From the former it may be distinguished by its longer calyx and corolla lobes, its calyx fused for 1/4 its length or less, its corolla tube no more than 5 times as long as the calyx, its corolla lobes more than twice as long as broad and longer in relation to the tube, and its stamens inserted at or above the apex of the calyx lobes. *L. peduncularis* may be distinguished from *L. jefensis* by its membranaceous leaves, its longer corolla, its longer corolla lobes, and its filaments and styles not, or only barely exceeding the corolla lobes.

I have collected *Lisianthius peduncularis* at El Valle, where it certainly is not common. Only a single small population was found. It is entirely possible that all the known specimens are from this population, and the population is merely an aberrant one of *L. skinneri*. However the presence of a specimen of *L. skinneri* from El Valle [*Allen 2369* (MO)], with no specimens intermediate toward *L. peduncularis* known from the area suggests otherwise. Although I do so with some reservation, I prefer to treat *L. peduncularis* as a species distinct from *L. skinneri*. Perhaps more adequate collections in the future will lead to a reconsideration.

12. **Lisianthius jefensis** Robyns & Elias, Ann. Mo. Bot. Gard. **55**: 60. 1968 (as *Lisianthus*). TYPE. **Panama.** PANAMA: Cerro Jefe, *Elias & Hayden 1798* (MO).

Slender shrubs, glabrous throughout. Stems 1.3–2.5 mm. tall and to 2 cm. in diameter, erect or the secondary branches ascending, terete, gray-brown below and green above. Leaves glossy dark green above, paler and dull below, the lateral nerves prominent, the blades (1.5)2.7–11.8 (20.6) cm. long and 0.8–5.0(7.7) cm. broad, narrowly obovate to oblanceolate and elliptic, widest at or above the middle, abruptly acuminate, the bases long-attenuate into the winged petiole. Inflorescences of pedunculate dichasia, these apparently simple (1-compound) but sometimes reduced to 1 or 2 flowers; flowering branches ascending, the axes terete or slightly flattened, once- or more rarely twice-ternately divided, each division terminated by a dichasium; branches and the stalks of the dichasia indistinctly 4-angled, elongate and the inflorescences loose and open. Flowers horizontal or nodding, the pedicels 0.7–2.5 cm. long; bracteoles subulate, scarious. Calyx 7–13 mm. long, fused for 1/3–2/5 its length; lobes 4.5–9 mm. long and 1.5–3 mm. broad, lanceolate to ovate-lanceolate, long-acuminate, scarious-margined, ridged or weakly carinate abaxially; tube 3–4 mm. long. Corolla tubular, 2.5–4.2 cm. long; tube 2.1–3.5 cm. long and 5–8 mm. broad at the broadest point, bright yellow with a greenish-yellow or dark green apex, constricted in the lower third, inflated in the midparts; lobes 4–6.5 mm. long and 1.5–3.5 mm. broad, 1/5–1/6 as long as the tube, spreading and recurved at the tips, greenish-yellow or dark green with paler margins, triangular-ovate to ovate-lanceolate, rather long acuminate. Stamens inserted on the corolla tube ca. 2/5 of the distance of the base to the apex; filaments 1.3–3 cm. long, exserted, the longest ones surpassing the corolla lobes; anthers 2.5–3.5 mm. long and 1–1.5 mm. broad, yellow, narrowly oblong, acutish, the connective slightly exserted. Style 2.2–3.6 cm. long, conspicuously surpassing the corolla lobes, always surpassing the filaments; stigma peltate. Capsule fusiform, conspicuously beaked, 1–1.8 cm. long, not including the 1.5–4.5 mm. long beak; the marcescent corolla not persisting until the seeds are shed. FLOWERING: Jan.–Sept. CHROMOSOME NUMBER: $n = 18$.

DISTRIBUTION: From 850–900 meters in cloud forest near the summit of Cerro Jefe on the Continental Divide in central Panama (MAP 5).

REPRESENTATIVE COLLECTIONS

Panama. PANAMA: slopes of Cerro Jefe on the road to La Eneida, *Weaver & Wilbur 2250* (A, BM, DS, DUKE, F, IJ, LL, MICH, MO, NY, S, UC, US); slopes of Cerro Jefe, along road from Cerro Azul, just before the turnoff to La Eneida, *Weaver & Wilbur 2243* (A, BM, DS, DUKE, F, IJ, LL, MICH, MO, NY, S, UC, US); Cerro Jefe, *Elias & Hayden 1798* (US; isotype).

Lisianthius jefensis is known from only one, low shrubby mountaintop in central Panama where it is one of the more conspicuous elements of the vegetation. It is closely related to both *L. skinneri* and *L. peduncularis*. It differs from *L. skinneri* in its coriaceous leaves, its longer calyx lobes, its corolla lobes more than twice as long as broad and longer in relation to the tube, its corolla tube less than 4 times as long as the calyx, its stamens inserted at or just above the apex of the calyx lobes, and its calyx in fruit more than 1/2 as long as the capsule. Populations of *L. jefensis* and *L. skinneri* have been collected less than 100 meters apart on Cerro Jefe; the populations appear to be perfectly distinct. That *L. jefensis* is merely a cloud-forest form of *L. skinneri* is thus ruled out. Both species were grown from seed in the greenhouse at Duke University and the differences in leaf texture remained constant.

The apparent distinctness of the populations on Cerro Jefe, in spite of their close sympatry, strongly supports the separation of the two as distinct species.

13. **Lisianthius adamsii** Weaver, Brittonia 22: 11. 1970. TYPE. **Jamaica.** ST. ANN: Douglas Castle, ca. 2 mi. n. of the Mason River Savannah, *Weaver 1293* (DUKE!).

Spindly shrubs or subshrubs, glabrous throughout. Stems erect, 0.2–2 m. tall and to 1.5 cm. in diameter, terete, green and herbaceous above, gray-brown and woody below, leafy nearly to the base. Leaves dull gray-green, thickish, the venation indistinct, the blades (5.8)8–15(17.6) cm. long and (1.9)2.5–5.5(6.6) cm. broad, broadly oblanceolate to obovate (elliptic), abruptly short-acuminate (acute), the bases attenuate into the winged, 0.5–2 cm. long petiole. Inflorescences of pedunculate, apparently simple dichasia, these occasionally reduced to 1 or 2 flowers; flowering branches 1–2-ternately divided, each division terminated by a dichasium or group of dichasia; inflorescence branches and stalks elongate and the inflorescences loose and open. Flowers nodding, the pedicels 0.8–4.5 cm. long; bracteoles scarious, subulate. Calyx 7–13 mm. long, fused for 1/6–1/3 its length; the lobes 5–9 mm. long and 1.5–2.5 mm. broad, lanceolate, acuminate, scarious-margined, ecarinate; the tube 1.5–4 mm. long. Corolla tubular-funnelform, 3.9–5.6 cm. long; the tube 2.7–3.6 cm. long and 8–11 mm. in diameter at the broadest point, constricted in the lower third, somewhat inflated, frequently unevenly, in the midparts,

MAPS 4–7. Distribution of *Lisianthius* species. MAP 4, *L. skinneri* (dots), *L. viscidiflorus* (triangles). MAP 5, *L. auratus* (dots), *L. jefensis* (half-circle), *L. pedunculares* (triangle). MAP 6, *L. acuminatus* (triangle), *L. axillaris* (dots). MAP 7, *L. seemannii*.

glossy clear yellow; the lobes 1.2–2 cm. long and 5–7 mm. broad, greenish-yellow, spreading and conspicuously recurved, ovate-lanceolate, abruptly short-acuminate. Stamens inserted on the corolla tube ca. 1/3 of the distance from the base to the apex; filaments 3–4 cm. long, exserted, at least the longest ones conspicuously surpassing the corolla lobes; anthers 2–4 mm. long and 1–2 mm. broad, oblong, acute, the connective exserted. Style 3.5–5.5 cm. long, surpassing the filaments; stigma peltate. Capsule oblong-ellipsoid, 14.5–16.5 mm. long and 5–7 mm. in diameter; the marcescent corolla persisting until the seeds are shed. FLOWERING: Feb.–Oct. CHROMOSOME NUMBER: $n = 18$.

DISTRIBUTION: From 500–750 meters in thickets and on rocky, limestone hillside in the central and western parishes of Jamaica (MAP 12).

SPECIMENS EXAMINED

Jamaica. CLARENDON: upper w. slope of Croft's Mountain, *Proctor 29234* (IJ). HANOVER: interior summit slopes of Dolphin Head, *Proctor 10037* (IJ). MANCHESTER: Somerset Woods, ca. 5 mi. nw. of Mandeville, *Proctor 16182* (A, BM, IJ). ST. ANN: Douglas Castle, ca. 2 mi. n. of the Mason River Savannah, *Weaver 1293* (GH, UCWI; isotypes).

Lisianthius adamsii, the most recently described species in the genus, is one of the more distinct and attractive of the species. With its coriaceous, gray-green, oblanceolate or obovate leaves; rather broad, inflated corolla tube and long recurved corolla lobes; and ecarinate calyx lobes, it is not easily confused with any other.

Vegetatively *Lisianthius adamsii* resembles somewhat *L. umbellatus* and *L. capitatus* (Series *Umbellati*), also with thickish, oblanceolate leaves; but it differs strikingly from them in its loose, open inflorescences and much longer corolla lobes. Although the relationships of *L. adamsii* are clearly with Series *Longifolii*, its specific relationships within the group are obscure. Its closest relatives are possibly the Jamaican *L. latifolius*, or, more probably, the Central American *L. skinneri*.

14. **Lisianthius acuminatus** Perk. Bot. Jahrb. 31: 493. 1902 (as *Lisianthus*). LECTOTYPE. **Mexico,** without exact locality, *Sumichrast 1558* (US!; a fragment).

Slender subshrubs, glabrous throughout. Lower portions of the stems unknown, the upper portions green, terete or indistinctly 4-angled. Leaves membranaceous, papillose above, the lateral veins prominent, the margins papillose, the blades 7.7–19.6 cm. long and 2.5–5.6 cm. broad, elliptic, abruptly long-acuminate, shortly attenuate and tapering into the winged petiole (to 4 mm. long). Inflorescences of pedunculate, apparently simple (1-compound) dichasia; flowering branches 1–2-ternately divided, each division terminated by a dichasium; axes of the flowering branches and the stalks and branches of the dichasia 4-angled, elongate and with the inflorescences diffuse; bracts subtending the dichasia green, linear. Flowers ascending, the pedicels 3–7 mm. long; bracteoles linear, scarious-margined

but usually green along the midline. Calyx 6.5–7.5 mm. long, fused for 1/5–1/3 its length; the lobes 4–6 mm. long and 1.5–2 mm. broad, lanceolate, acuminate, scarious-margined, distinctly carinate; the tube 1.5–2.5 mm. long. Corolla tubular, 3.4–3.7 cm. long; the tube 2.9–3.2 cm. long, yellow; constricted in the lower third, the lobes 4.5–5.5 mm. long and 2.5–3 mm. broad, 1/8–1/6 as long as the tube, slightly spreading, greenish-yellow, ovate, acute or abruptly short-acuminate. Stamens inserted on the corolla tube ca. 1/2 of the distance from the base to the apex; filaments 2.1–2.7 cm. long, surpassing the corolla tube but not the lobes; anthers ca. 2.5 mm. long and 1.5 mm. broad, broadly oblong, the connective very barely exserted. Styles ca. 3 cm. long, exceeding the corolla lobes, always exceeding the filaments; stigmas peltate. Capsule not seen.

DISTRIBUTION: Near Orizaba in south-central Mexico (MAP 6).

SPECIMENS EXAMINED

Mexico: without exact locality, *Sumichrast 1558* ✓(K; lectotype collection), photograph (DUKE). VERACRUZ: Orizaba, *Botteri* (GH); Monte San Cristobal, Orizaba, *Mohr & Botteri* (US).

Lisianthius acuminatus is one of the most poorly understood and rarely collected of the species. Only 2 specimens, in addition to a fragment of the lectotype and a photograph of an isolectotype, the most recent collected in 1866, were available for study. *L. acuminatus* appears to be most closely related to the Jamaican *L. latifolius* or perhaps to the alliance of West Indian species that includes *L. troyanus*, *L. laxiflorus*, and *L. glandulosus*. Of the Mexican and Central American species *L. acuminatus* might possibly be confused with *L. quichensis* in subsect. HERBACEI. However that plant is a suffrutescent herb with a determinate main axis. In addition, the corolla tube of *L. quichensis* is somewhat inflated and broadest below the apex, the corolla lobes are erect, and the filaments exceed the corolla lobes.

In the original description of *Lisianthius acuminatus*, Perkins cited two specimens as representative of the new taxon. These specimens (*Sumichrast 1558* and *1856*), which must be treated as syntypes, were presumably at Berlin and destroyed during World War II. There is however a duplicate of *Sumichrast 1558* at Kew, a photograph of which (DUKE) I have seen. In addition Perkins sent a fragment of *Sumichrast 1558* to John Donnell Smith according to a letter from her dated 31 March 1910 and presently attached to *Heyde & Lux 2921* (US), the holotype of *L. quichensis*. This fragment includes a leaf, a bud, and the upper portion of the corolla of a nearly mature flower. The fragment, along with the original description, serves to identify Perkins' plant; since it is all that remains of the original material, the fragment of *Sumichrast 1558* (US) is designated the lectotype of *L. acuminatus* Perkins.

15. **Lisianthius auratus** Standl. Trop. Woods 37: 29. 1934 (as *Lisianthus*). ✓TYPE. **Honduras.** COMAYAGUA: open mountain forests, Siguatepeque, *Edwards P–556* (F!).

Slender subshrubs, glabrous throughout. Stems 0.5–2.5 m. tall and to 1 cm. in diameter, erect or reputedly sprawling, green or brown at base, terete below but indistinctly 4-angled above. Leaves thin-membranaceous, dull dark green above and paler beneath, the principal lateral veins evident on both surfaces, on drying the veinlets occasionally conspicuous, the blades 2.1–11.5 cm. long and 0.8–3.6 cm. broad, ovate-lanceolate or ovate or tending toward elliptic, long-acuminate, rounded, or short-attenuate at base, the upper ones and those on the secondary branches more distinctly lanceolate and rounded at base; petioles 3–8 mm. long. Inflorescences of pedunculate, apparently simple dichasia, these frequently reduced to 1 or 2 flowers. Flowering branches with a terminal and 1–3 pairs of axillary dichasia; axes of the flowering branch and the dichasial branches 4-angled. Flowers nodding or almost pendent, the pedicels 0.6–1.7 cm. long; bracteoles scarious, subulate. Calyx 5–10 mm. long, fused for 2/10–3/10 its length; the lobes 3.5–7.5 mm. long and 1–2 mm. broad, lanceolate, long-acuminate, scarious margined, weakly carinate abaxially; the tube 1.5–2.5 mm. long. Corolla tubular-funnelform, uniformly yellow, 2.9–4.0 cm. long; the tube 2.2–3.0 cm. long and 4.5–7.5 mm. broad; constricted in the lower half, the lobes 5–11 mm. long and 3–4.5 mm. broad, 1/4–3/8 as long as the tube, spreading but not recurved, ovate-lanceolate, cuspidate-acuminate. Stamens inserted in the lower 1/4–1/3 of the corolla tube; filaments 2.0–3.0 cm. long, the longer ones exceeding the corolla lobes, and often equalling the style; anthers 2–2.5 mm. long and 1–1.5 mm. broad, narrowly oblong, the connective slightly exserted. Style 2.4–3.6 cm. long, surpassing the corolla lobes; stigma capitate. Capsule 8–12 mm. long and 3–5 mm. broad, oblong-ellipsoid, short-beaked; the marcescent corolla not persisting until the seeds are shed. FLOWERING: All year. CHROMOSOME NUMBER: $n = 18$.

DISTRIBUTION: From near sea level to 1800 meters in pine forests or savannahs at scattered localities from western British Honduras to southeastern Guatemala, and west-central Honduras to northeastern Nicaragua (MAP 5).

SPECIMENS EXAMINED

British Honduras. CAYO DIST.: 3 mi. n. of Augustine on the banks of the Río No, Mountain Pine Ridge, *Weaver & Wilbur 2253* (A, DUKE, F, MICH, MO); Augustine, Mountain Pine Ridge, near Río Frío, *Hunt 401* (BM, F, LL, US); **Guatemala.** CHIQUIMULA: Cerro Tixixi, 3–5 mi. n. of Jocotán, *Steyermark 31603* (F). **Honduras.** COMAYAGUA: open pine forests, Siguatepeque, *Edwards 556* (US; isotype); Barranco El Soccoro, mountains about 8 km. w. of Siguatepeque, *Williams & Williams 18382* (GH, F); trincheras, 20 km. n. of Siguatepeque, *Howard et al. 628* (A). INTIBUCHA: paredones humedos de la Cascada de Yamaranquila, *Molina 6358* (US); Barranco Yamaranquila, cerca de Yashse, *Molina 6524* (US). **Nicaragua.** COMARCA DE EL CABO: Río Leícus 28 km. so. de Waspan, *Molina 15206* (F); bosque de la Quebrada Cuyu, *Molina 15037* (F); matorrales de Río Leícus cerca del campo de aviación de Tronquera, 35 km. so. de Waspan, *Molina 15171* (F).

Of the Central American species of *Lisianthius*, *L. auratus* appears to be most closely related to *L. axillaris*, a fact recognized by Standley when he described *L. auratus*. Although they have occasionally been confused, *L. axillaris* differs strikingly from *L. auratus* in having red flowers almost invariably borne singly in the axils of the foliage leaves. *L. auratus* strongly resembles certain of the West Indian species especially the *L. troyanus* alliance, and is probably quite similar to the stock from which they evolved.

[*To be concluded*]

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COVER: A CENTURY OF TREES.

The cover design was planned and drawn by Karen Stoutsenberger Velmure especially for the *Journal of the Arnold Arboretum*. It will be used during 1972 to celebrate the Centennial Year of the Arnold Arboretum of Harvard University. The design consists of one hundred trees representing the range and diversity of the collections of the Arboretum.

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A REVISION OF THE NEOTROPICAL GENUS LISIANTHIUS (GENTIANACEAE)

≠ 006879

RICHARD E. WEAVER, JR.*

16. **Lisianthius troyanus** Urb. Symb. Antill. 6: 32. 1909 (as *Lisianthus*). LECTOTYPE. **Jamaica:** near Troy, *Harris 8789* (NY!).

Slender subshrubs, glabrous throughout. Stems 0.5–1.5 m. tall and to 1 cm. in diameter, erect or ascending, terete, green above and gray-brown below. Leaves membranaceous, the principal lateral veins prominent, glossy grass-green above, paler and dull beneath, the blades 2.9–12(16.8) cm. long and 0.7–4.9 cm. broad, 3–4 times as long as broad, elliptic (usually narrowly so) to oblanceolate, broadest at or above the middle, the apices short-acuminate (long-acuminate or acute), the bases long-attenuate and tapering into the narrowly winged, 0.5–2.5 cm. long petiole. Inflorescences of apparently simple dichasia, these sometimes reduced to single flowers; flowering branches 1–2-ternately divided; inflorescence branches and stalks terete, elongate and the inflorescences diffuse. Flowers nodding, pedicels slender, 3–19 mm. long; bracteoles subulate, scarious. Calyx (4)5.5–10.5(12) mm. long, fused for 1/8–1/4 its length; the lobes 3–9(11) mm. long and 1–1.5 mm. broad, lanceolate or subulate-lanceolate, long acuminate, scarious-margined, ridged abaxially; the tube 1–3 mm. long. Corolla 3.3–4.6 cm. long, tubular-funnelform, uniformly bright yellow; tube 2.2–3.3 cm. long and 5–7.5 mm. in diameter at the apex, constricted in the lower 1/3–2/5; lobes 9–14 mm. long and 2.5–4.5 mm. broad, widely spreading, ovate-lanceolate or lanceolate, abruptly short-acuminate (to gradually acuminate), 1/3–2/5(1/2) as long as the tube. Stamens inserted on the corolla tube 1/3–2/5 of the distance from the base to the apex; filaments 1.9–3 cm. long, not exceeding the corolla lobes but rarely almost equalling them; anthers 1.5–2.5 mm. long and 1–1.5 mm. broad, narrowly oblong, acutish, the connective slightly exserted. Styles 2.4–3.7 cm. long, exceeding the filaments, slightly surpassing the corolla lobes or not; stigmas capitate, distinctly bilobed. Capsules oblong-ellipsoid, 8–12 mm. long, not including the 1–2.5 mm. long beak, and 2.5–4 mm.

* Continued from volume 53, p. 272.

in diameter; the marcescent corolla not persisting on the mature capsule. FLOWERING: All year. CHROMOSOME NUMBER: $n = 18$.

DISTRIBUTION: From 90 to 600 meters on rocky limestone hillsides or roadside banks in western Jamaica (MAP 10).

REPRESENTATIVE COLLECTIONS

Jamaica. near Troy, *Harris 8789*✓(UCWI; isotype); Cockpit Country, Troy, *Britton 509* (NY); Cockpit Country, near Balaclava, *Marble 923* (NY). HANOVER: Cocoa Walk District, W side of the Hanover Hills, near the Great Morass, Farr s.n. (IJ, NY); Houghton Mtn. District, 0.5 mi. S of Cave Valley, *Proctor 11295* (IJ). WESTMORELAND: 0.5 mi. S of Moreland Hill School, *Weaver & Weaver 1272* (A, BM, DUKE, F, LL, MICH, MO, S, UCWI, US).

Lisianthius troyanus, a rather uncommon species, is probably most closely related to the Puerto Rican *L. laxiflorus* and the Cuban *L. glandulosus*. It resembles these species strongly in most respects, particularly in its capitate, distinctly bilobed stigmas, but it should not be confused with them since the ranges of all three species are distinct. Of the Jamaican species, *L. troyanus* most closely resembles *L. latifolius*. That species differs however in its peltate stigmas, its corolla tubes not conspicuously constricted in the basal portion, its styles and filaments never exceeding the corolla lobes, and its broader leaves; in addition *L. latifolius* is restricted to the cloud forests and elfin woodland in the mountains of eastern Jamaica while *L. troyanus* is found on dry limestone hillsides of western Jamaica at an elevation below 700 meters.

The holotype of *Lisianthius troyanus*, along with most of Urban's type material was destroyed during the bombing of Berlin during World War II (H. Scholz, *in litt.*). However, I have seen 2 isotypes (NY, UCWI). Of these, the specimen at the New York Botanical Garden is more complete and better exhibits the characters described by Urban. Therefore, *Harris 8789* (NY) is designated the lectotype of *L. troyanus* Urb.

The specimens of *Lisianthius troyanus* from the vicinity of Troy in the Cockpit Country, including the type collection and two additional ones, differ slightly from those specimens from the far western parishes of Jamaica. These latter specimens are distinguished from the typical element by having corolla lobes abruptly acuminate and slightly shorter in relation to the tube, generally shorter calyx lobes, and styles surpassing the corolla lobes. Although there is an overlap in all the critical characters, plants of the two groups of populations look slightly different from herbarium specimens. However the paucity of material at hand makes critical evaluation of their relationships difficult. Until more material is available, particularly from the region between the presently known distributions of these groups of populations, I prefer to make no formal distinction between them.

17. **Lisianthius glandulosus** A. Rich. *in* Ramon de la Sagra, Hist. Isla de Cuba 11: 102. 1850 (as *Lisianthus*). TYPE. **Cuba:** Sierra Maestra, St. Yago de Cuba, *Linden 2014* (P!).

L. stenophyllus Urb. Symb. Antill. **9:** 237. 1924. TYPE. **Cuba.** ORIENTE: Sierra Maestra, Pinar del Papayo, *Ekman 9269* (s!).

Slender subshrubs, glabrous or minutely spiculate. Stems 0.2–1 m. tall and to 5 mm. in diameter, slender, erect or ascending, glabrous or rarely minutely spiculate, especially above, brown and terete below, green and 4-angled above. Leaves membranaceous, the venation not particularly conspicuous; foliage leaves subsessile or short-petiolate, the blades (1.5) 2.3–10.5 cm. long and (0.2)0.8–4.2 cm. broad, elliptic to very narrowly elliptic to ovate-lanceolate, widest at or below the middle, 2–10 times, but usually less than 6 times, as long as broad, gradually acuminate at the apex, the base obtuse or shortly attenuate into the short, winged

MAP 8. Distribution of *Lisianthius* species. *L. domingensis* (squares), *L. glandulosus* (half-circles), *L. silenifolius* (dots).

petiole; petioles to 7 mm. long. Inflorescences of long-pedunculate, apparently simple (1-compound) dichasia, occasionally reduced to 1–2 flowers; flowering branches 1–2-ternately divided, each division terminated by a dichasium or a reduced dichasium; axes of the flowering branches and inflorescences strongly angled, the angles frequently expanded into narrow, scarious wings. Flowers nodding, frequently strongly, the pedicels relatively stout (3)8–13(20) mm. long; bracteoles subulate or linear, scarious. Calyx (5)6.5–12 mm. long, the lobes (4.5)5.5–10.5 mm. long and 1–2 mm. broad, narrowly lanceolate, long-acuminate, scarious-margined, weakly carinate abaxially. Corolla (2.4) 2.9–3.8 cm. long, tubular-funnelform, uniformly bright yellow; the tube (1.9)2.2–3.2 cm. long and 3–6 mm. in diameter at apex, tightly constricted in the lower half, 3 times (or more) as long as the calyx; the lobes 5–9 mm. long and 2–4 mm. broad, spreading, narrowly ovate, abruptly or gradually short-acuminate (acute), 2/10–3/10 as long as the tube. Stamens inserted above the apex of the calyx lobes; filaments 1–2.2 cm. long, never exceeding the corolla lobes, the longer ones usually equalling the style; anthers 1.5–2 mm. long and ca. 1 mm. broad, oblong, obtuse. Style 1.5–2.5 cm. long. Capsule fusiform or oblong-ellipsoid, short-beaked, 8–15 mm. long, not including the 1–2 mm. long beak, and 2–4 mm. in diameter; calyx in fruit 1/3–2/3 as long as the capsule; the marcescent corolla sometimes persisting until the seeds are shed. FLOWERING: All year.

DISTRIBUTION: From 300 to 1500 meters in pinelands or in moist limestone forests in the mountains, particularly the Sierra Maestra, in Oriente Province in eastern Cuba (MAP 8).

REPRESENTATIVE COLLECTIONS

Cuba: without locality, *Linden 2014* (BM; isotype). ORIENTE: Sierra Maestra, Pinar del Papayo, *Ekman 9269* (S; type of *L. stenophyllus*), supra Daiquiri, *Ekman 8174* (MICH, S), Loma del Gato, *Ekman 7004* (S), Gran Piedra, *Shafer 9058* (NY, US), Pico Turquino, *Seifriz 1075* (US), w. of Rio Yao, *Morton & Acuña 3429* (US), foothills on n. side of La Bayamesa, *Webster 4078* (MICH, US); Pico del Cristal, *Lopez 81* (US); Baracoa, pinelands on way to Florida, *Ekman 3992* (F, MICH, S, UC, US); at the top of El Yunque, *Ekman 3976* (F, S, US); minas de Iberia ad Taco Bay, *Ekman 3807* (S); on Vía Azul, between Sabanilla and Cajobabo, at km. 22 from Sabanilla, *Morton & Alain 9000* (US); Camp La Gloria, s. of Sierra Moa, *Shafer 8081* (NY); Sabanilla to Yumuri Arriba, *Shafer 8409* (NY, US); vicinity of El Cuero, *Britton & Cowell 12768* (NY); Arralo de Medio, *Shafer 3258* (NY); Sierra del Nipe, Loma Mensura, *Ekman 5743* (S); Corojo, "Treinta Pinos," *Ekman 5178* (S).

Lisianthius glandulosus is probably most closely related to the Jamaican *L. troyanus* and the Puerto Rican *L. laxiflorus*. It differs from both of these species in its corolla lobes which are less than 1/3 as long as the tube. It differs further from *L. troyanus* in its strongly 4-angled inflorescence branches and its style never exceeding the corolla lobes. It differs further from *L. laxiflorus* in that its corolla tube is 3 times or more longer than the calyx.

Although Perkins (1902) considered it a synonym of *Lisianthius glandulosus*, *L. silenifolius*, the only other Cuban species, differs strongly in that it is an annual or perennial suffrutescent herb with inflorescences of compound dichasia, sessile leaves, and ovoid capsules. *L. silenifolius* is here placed in subsect. HERBACEI of sect. LISIANTHIUS.

In the protologue of *Lisianthius stenophyllus*, Urban stated that his new species is distinguished from the other Antillean species by its narrow leaves. *L. stenophyllus* is known from only the two specimens of the type collection, *Ekman 9269*, and these specimens indeed have leaves narrower than any found elsewhere in the genus. The leaves are at least 8 times longer than broad. However, except for being more densely spiculate, *Ekman 9269* is identical to *L. glandulosus* in its other features. Since leaf shape is a widely variable character throughout the genus, *L. stenophyllus* is not maintained as a distinct species. Its apparent sympatry with *L. glandulosus* would prevent me from treating it as a variety of that species. Therefore, at least until more material is available, I consider it to be a slightly aberrant population of *L. glandulosus*.

18. **Lisianthius laxiflorus** Urb. Symb. Antill. 3: 332. 1902 (as *Lisianthus*). LECTOTYPE. **Puerto Rico**: prope Peñuelas ad montem Las Cruces, *Sintenis 4386* (UCWI!).

† *Lisianthus gracilis* sensu Perkins, Bot. Jahrb. 31: 493. 1902, not *Leianthus* (= *Lisianthius*) *longifolius* β *gracilis* Griseb.

Spindly subshrubs, glabrous throughout. Stems 0.3–1 m. tall and to 5 mm. in diameter, erect or ascending, or reputedly climbing, brown and more or less terete below, green and angled above. Leaves thin-membranaceous, the principal lateral veins and often the veinlets evident, at least upon drying; leaves 2.6–9.7 cm. long and 0.4–3.1 cm. broad, lanceolate (or ovate-lanceolate), broadest below the middle, the apices gradually long-acuminate, the bases obtuse or short-attenuate and tapering into the short, winged petiole, subsessile or the petioles to 5 mm. long. Inflorescences of long-pedunculate, apparently simple (1-compound) dichasia, often reduced to 1 or 2 flowers; flowering branches typically 1–2-ternately divided, the divisions terminated by dichasia, the lateral ones 1–(2–3)-flowered, the terminal one (1)2–3-flowered; axes of the flowering branches and inflorescences strongly 4-angled, the angles typically expanded into narrow, scarious wings. Flowers nodding, the pedicels relatively slender (0.3)1.1–2.2(2.8) cm. long; bracteoles foliaceous or more rarely nearly scarious, linear to narrowly elliptic, 2–8(10) mm. long. Calyx 8–13.5 mm. long, fused for 1/8 its length or less; the lobes 7–12 mm. long and 1–2 mm. broad, narrowly lanceolate, long-acuminate, ridged abaxially, essentially green but with narrow, scarious margins; the tube 0.5–2 mm. long. Corolla 3.0–4.5 cm. long, deeply cleft, funnelform, uniformly bright yellow; the tube 1.8–2.5 cm. long and 4–7 cm. in diameter at the apex, slightly constricted in the lower 1/3–1/2; the lobes 1.2–2 cm. long and 2–4 mm. broad, 6/10 as long to nearly as long as the tube, spreading or perhaps slightly recurved, elliptic-lanceolate or lanceolate, gradually long-acuminate. Stamens inserted on the corolla tube one half or just less than half the distance from base to apex; filaments 1.4–2.5 cm. long, reaching to about the midpoint on the corolla lobes, occasionally equalling the style; anthers 1.5–2.5 mm. long and ca. 1 mm. broad, oblong, obtuse or acutish. Styles 1.9–2.7 cm. long; stigmas capitate, distinctly bilobed. Capsule fusiform, short-beaked, 7–15 mm. long, not including the 1 mm. long beak, and 2.5–4 mm. in diameter; calyx in fruit nearly equalling capsule; the marcescent corolla occasionally persisting until the seeds are shed. FLOWERING: Dec.–July.

DISTRIBUTION: From 300 to 1300 meters in moist forests or along roadsides in the mountains of Puerto Rico (MAP 9).

REPRESENTATIVE COLLECTIONS

Puerto Rico: Peñuelas, inter frutices ad Las Cruces, *Sintenis 4386* (F, GH, MO, NY, S, UCWI, US; isolectotypes); Maricao, *Sintenis 202* (BM, GH, S, US; cited collection); Yauco, *Garber 64* (GH, NY; cited collection); 14 mi. ne. of Mayagüez, *Heller 4474* (F, GH, MICH, MO, NY, US; cited collection): Lares, ad Buenos Aires, *Sintenis 6077* (BM, US; cited collection); prope Utuado. *Sintenis 6424* (BM, GH, NY, US; cited collection); south side of El Yunque Mtn., *Blomquist 13195* (DUKE, MO); km. 15 on El Yunque Road from Palmer to Florida, *Wagner 2* (A); Route 191, km. 17.2 on south side of the Luquillo Mountains, *Wagner 1802* (DUKE); Río de Maricao, *Britton & Cowell 4228* (F, MO, NY, US); Maricao Forest, near radar site, *Howard & Nevling 15349* (A); Cerro Gordo,

San German, *Vélez 1426* (GH); mountains of Toro Negro, Cerro de Punta, *Alain 9480* (IJ); Sierra de Naguabo, *Shafer 3528* (F, MO, NY, US).

Lisianthius laxiflorus, the only species in the genus known from Puerto Rico, is most similar to the Jamaican *L. troyanus* Urb., from which it differs in its 4-angled inflorescence branches, its lanceolate leaves, its corolla lobes 3/5–9/10 as long as the tube, and in its distribution.

In her treatment of *Lisianthius*, Perkins (1902) included a plant which she called *Lisianthus gracilis* (Griseb.) Perk., citing as the basionym *Leianthus longifolius* (L.) Griseb. var. *gracilis* Griseb. (Fl. Brit. W. Ind. Isl. 421. 1862). From the specimens she cited, all Puerto Rican, it is obvious that this plant is the same as *Lisianthius laxiflorus* Urb. In fact, all of these specimens were cited slightly later by Urban as representative of *L. laxiflorus*.

In his treatment of *Leianthus longifolius* (= *Lisianthius longifolius* L.) Grisebach (1862) recognized 3 varieties: α (the typical one), β *gracilis*, and γ *cordifolius*. No authentic material of Grisebach's has been seen; his description of β *gracilis* is brief and could equally well apply to some specimens of the Jamaican *Lisianthius longifolius*, as well as to *L. laxiflorus* or the Cuban *L. glandulosus*. However, in his comprehensive description of *Leianthus longifolius*, Grisebach (loc. cit.) states that the corolla tube is "twice or thrice" as long as the lobes. *Lisianthius laxiflorus* is thus excluded, since in this species the corolla tube is less than twice as long, and usually less than 1.5 times as long, as the lobes. In addition, Grisebach (loc. cit.) gave the distribution of *Leianthus longifolius* as Jamaica and Cuba; *Lisianthius laxiflorus* is restricted to Puerto Rico.

From the description, then, *Leianthus longifolius* (including var. *gracilis*) as circumscribed by Grisebach (1862) does not include the Puerto Rican material. Therefore, since Perkins' *Lisianthus gracilis* was based on Grisebach's *Leianthus longifolius* var. *gracilis*, Urban was correct in applying a new name to the Puerto Rican *Lisianthius*.

In describing *Lisianthius laxiflorus* Urban cited 9 specimens as representative of his new species. Although most of these were destroyed during World War II (H. Scholz, *in litt.*), there is reason to believe that at least one specimen of *L. laxiflorus* seen by Urban is extant. Among the collections at the University of the West Indies in Mona, Jamaica, is a specimen of *Sintenis 4386*, the label of which, including the word "typus," is written in Urban's hand as determined by Dr. C. D. Adams of that university. The locality data on this specimen, "Prope Peñuelas ad montem Las Cruces," compares favorably with an entry, "Peñuelas in monte Las Cruces," in Urban's protologue of *L. laxiflorus*. In addition, this specimen was annotated by Perkins, as *Lisianthus gracilis* (Griseb.) Perk., in 1901, the year before the original description of *L. laxiflorus* was published. Since both Perkins and Urban worked at Berlin-Dahlem, it is quite possible that Urban saw this specimen.

Twelve additional specimens of *Sintenis 4386* have been seen. The labels

of these were not written in Urban's hand and the locality data ("Peñuelas, inter frutices ad Las Cruces") differ from those of the above-mentioned specimen.

Until proved otherwise, I consider the specimen of *Sintenis 4386* (UCWI) from "Prope Peñuelas ad montem Las Cruces" to be the only cited specimen probably seen by Urban, and I designate it the lectotype of *Lisianthius laxiflorus* Urb.

19. **Lisianthius latifolius** Sw. Prodr. 40. 1788; Fl. Ind. Occ. 1: 348. 1797 (as *Lisianthus*). LECTOTYPE. **Jamaica,** without exact locality, *Swartz* (S!).

Leianthus latifolius (Sw.) Griseb. Gen. & Sp. Gent. 199. 1839 [1838].

Slender shrubs or subshrubs, glabrous throughout. Stems 0.3–2 m. tall and to 1.5 cm. in diameter, erect or ascending, terete, green and herbaceous above, gray-brown and woody below. Leaves firmly membranaceous, the principal lateral veins usually prominent, glossy grass-green or rather dark green above, paler and dull beneath, the blades (3.6)5–17(21.6) cm. long and (1.5)2–7 cm. broad, 2.5 to 4 times as long as broad, elliptic or oblong elliptic (obovate), widest at or above the middle, long-acuminate, the bases attenuate into the winged (0.3)1–4.2 cm. long petiole. Inflorescences of pedunculate, apparently simple dichasia, or occasionally reduced to solitary, axillary flowers; flowering branches 1–2-ternately divided, each division terminated by a dichasium, with 1–3 pairs of reduced leaves below the first division; inflorescence branches terete, elongate, and the inflorescences diffuse. Flowers nodding, pedicels relatively stout (0.6) 1–2.6 cm. long; bracteoles subulate, scarious. Calyx 6–14 mm. long, fused for 1/5–1/4 its length; lobes 4.5–10.5 mm. long and 1.5–2 mm. broad, lanceolate, long-acuminate, pale green, scarious-margined, ridged abaxially; the tube 1.5–3 mm. long. Corolla funnelform, 3.5–5.5 cm. long; the tube 2.2–3.9 cm. long and 7–10 mm. broad at the apex, bright yellow, slightly constricted in the lower third; lobes 11–18 mm. long and 3.5–6 mm. broad, greenish-yellow, spreading or weakly recurved, ovate-lanceolate or oblong-lanceolate, acute or abruptly short-acuminate, 2/5–1/2 as long as the tube. Stamens inserted on the corolla tube 1/3–2/5 of the distance from the base to the apex; filaments 1.9–2.9 cm. long, not exceeding the corolla lobes; anthers 2–3.5 mm. long and 1–2 mm. broad, broadly oblong, obtuse, the connective not at all exserted. Ovary fusiform; style 2.5–4.2 cm. long, never equalling the corolla lobes; stigma peltate. Capsule oblong-ellipsoid to fusiform, long beaked, 10–17 mm. long, not including the 3–7 mm. long beak, and 4–6 mm. in diameter; the marcescent corolla never persisting on the mature capsule. FLOWERING: All year. CHROMOSOME NUMBER: $n = 18$.

DISTRIBUTION: From 600–2100 meters in cloud forests and elfin woodland in the Blue Mountains and the John Crow Mountains in eastern Jamaica (MAP 10).

REPRESENTATIVE COLLECTIONS

Jamaica. "Ind. occ.", *Swartz* (S); without locality, *Swartz* (BM; isolectotype); without locality, *MacFadyen* (GH). PORTLAND: west slope of Silver Hill, *Anderson & Sternberg 3259* (DUKE); Sir John Peak, *Shreve s.n.* (NY); Morces Gap, *Weaver 1827* (A, BM, DUKE, F, MICH, MO, UCWI, US); east slope of the John Crow Mtns., 1.5–2 mi. sw. of Ecclesdown, *Proctor 9990* (IJ). ST. ANDREW: along ridge between Morces Gap and John Crow Peak, *Proctor 9517* (IJ); John Crow Peak, *Shreve* (NY). ST. THOMAS: trail from Portland Gap to Blue Mtn. Peak, *Weaver 1952* (DUKE); Portland Gap, *Weaver 1953* (A, DUKE, UCWI); near summit of Sugar Loaf Peak, *Farr* (IJ); summit of High Peak, *Lewis* (IJ).

Lisianthius latifolius is probably most closely related to *L. domingensis*, from the island of Hispaniola, but the two should not be confused since they have different distributions and clear cut morphological differences. No other species of *Lisianthius* is found in the cloud forests and elfin woodland in the Blue Mountains of Jamaica. Of the Jamaican species, *L. latifolius* most closely resembles *L. troyanus* Urb. The latter species differs, however, in its styles usually exceeding the corolla lobes, its corolla tubes conspicuously constricted in the basal portions, its stigmas capitate, and the beaks of its capsules less than 1/4 as long as the capsules.

In Swartz's herbarium at Stockholm (S) are three specimens of *Lisianthius latifolius*, two inscribed "Ind. occ." and one inscribed "Jamaica." One of the former specimens and also the latter one include a single, unattached flower of *L. longifolius*. Of these specimens the one inscribed "Jamaica" best demonstrates the characters described by Swartz and, excluding the fragment of *L. longifolius*, is here designated the lectotype of *L. latifolius* Sw.

20. **Lisianthius domingensis** Urb. Symb. Antill. 3: 333. 1902 (as *Lisianthus*). LECTOTYPE. **Haiti:** Gonaives, Morne Fourmi, *Buch 761* (IJ!).

Spindly subshrubs, glabrous throughout. Stems 0.4–1 m. tall and to 5 mm. in diameter, erect or ascending, terete, brown below but green above. Leaves membranaceous, the principal lateral veins prominent, at least below, subsessile to distinctly petiolate, the blades 1.8–7.5 cm. long and 0.8–3.1 cm. broad, narrowly ovate to broadly elliptic, abruptly short acuminate to gradually acuminate, the bases more or less rounded to cuneate, or attenuate into the winged petiole; petioles, when present, to 10 mm. long. Inflorescences of reduced dichasia, these 1- or more rarely 2-flowered. Flowers nodding, the pedicels relatively stout, 0.3–2 cm. long; bracteoles 1.5–10 mm. long, narrowly-elliptic to linear-subulate, typically foliaceous but rarely nearly scarious. Calyx 5.5–9.5 mm. long, fused for 2/10–3/10 its length; the lobes 4–7.5 mm. long and 1–2 mm. broad, lanceolate, acuminate, ridged abaxially, with very narrow, scarious margins; the tube 1–3 mm. long. Corolla 2.9–4.4 cm. long, tubular-funnelform,

MAPS 9–13. Distribution of *Lisianthius* species. MAP 9, *L. laxiflorus*. MAP 10, *L. longifolius*. MAP 11, *L. capitatus* (dots), *L. umbellatus* (squares). MAP 12, *L. latifolius* (dots), *L. troyanus* (squares). MAP 13, *L. adamsii* (squares), *L. cordifolius* (dots), *L. exsertus* (half-circles).

uniformly bright yellow; the tube 2.3–3.1 cm. long, slightly constricted in the lower third; lobes 0.8–1.6 cm. long and 2.5–4 mm. broad, oblong-lanceolate, acute or short-acuminate, spreading or perhaps recurved, ca. 1/2 as long as the tube. Stamens inserted on the corolla tube ca. 2/5 of the distance from the base to the apex; filaments 1.5–2.4 cm. long, equalling the corolla tube or slightly surpassing it, often equalling the style; anthers oblong, 1.5–2 mm. long and ca. 1 mm. broad. Style 1.6–2.6 cm. long; stigmas peltate. Capsule oblong-ellipsoid, beaked, 11–14 mm. long, not including the 1–3 mm. long beak, and 3.5–5 mm. in diameter; the marcescent corolla sometimes persisting until the seeds are shed. FLOWERING: Dec.–Apr.

DISTRIBUTION: From 900 to 1500 meters in wet, mossy forests in the Cordillera Central of the Dominican Republic and the Massif du Nord of Haiti (MAP 8).

SPECIMENS EXAMINED

Haiti: Gonaives, Morne Fourmi, *Buch 761* (GH; isotype); road from Camp #1 to La Barrière Couchant, *Nash & Taylor 1096* (NY); Massif du Nord, Ld. Louis du Nord, Morne Baron, *Ekman 3889* (S); Port Margot, Morne Maleuvre, *Ekman 2817* (S). **Dominican Republic.** SANTO DOMINGO: Cordillera

Central, Loma la Campana, *Ekman 11516* (NY, S, US). TRUJILLO VALDEZ: Los Guineos, San Cristóbal, *Marcano 3658* (US).

Lisianthius domingensis, the only species known from the island of Hispaniola, is very poorly collected. It most closely resembles the Jamaican *L. latifolius*, both in morphology and habitat preference. That species differs, however, in its terete inflorescence branches, its usually 3-flowered dichasia, its long-beaked capsules, its broader leaves, and of course, its distribution.

The type of *Lisianthius domingensis*, along with most of Urban's type material, was destroyed during the bombing of Berlin in World War II (H. Scholz, *in litt.*). Two isotypes (GH, IJ) have been seen. Of these, only the specimen at the Institute of Jamaica includes flowers. Since it is the more complete of the known isotypes and the one which better demonstrates the characters described by Urban, *Buch 761* (IJ!) is designated the lectotype of *L. domingensis* Urb.

The Haitian plants, including the type collection, differ slightly in leaf morphology from the plants of the Dominican Republic. The Dominican plants are distinguished from the typical element by having leaves usually more rounded at the base and subsessile. These differences are minor and not entirely consistent, and especially in view of the lack of material at hand, represent insufficient grounds for formal recognition of the two groups of populations as distinct taxa.

21. **Lisianthius axillaris** (Hemsl.) O. Ktze. Rev. Gen. Pl. 2: 429. 1891.

Leianthus axillaris Hemsl. Biol. Centr. Am. Bot. 2: 344. 1882. TYPE. **British Honduras**: without exact locality, *Barlee* (DUKE, photo.!; K, holo.).

Lisianthus francisiae Sprague, Kew Bull. **1929**: 8. 1929. TYPE. **British Honduras:** Corozal, *Francis 1* (DUKE, photo.!; K, holo.).

Subshrubs, glabrous throughout. Stems terete, green, or brown near the base, erect or ascending, or the lateral ones spreading. Leaves membranaceous, shiny green above and duller below, the blades 1.6–13.8 cm. long and 0.9–5.1 cm. broad, elliptic (ovate), short-acuminate (acute), the bases shortly attenuate, subsessile or short-petiolate, the petioles then winged and to 8 mm. long. Flowers borne singly in the axils of the foliage leaves, usually opposite, rarely in axillary, short-pedunculate monochasia or dichasia, the peduncles then 0.5–4.5 cm. long. Pedicels 0.9–3.0 cm. long, ascending or horizontal, becoming recurved with age; bracteoles subulate, scarious. Calyx 8.5–13.5 mm. long, fused for 1/5–1/6 its length; lobes 7–11.5 mm. long and 1.5–3 mm. broad, lanceolate, very long-acuminate, scarious margined, keeled abaxially, the keel to 0.5 mm. broad; tube 1.5–2.5 mm. long. Corolla tubular-funnelform, 3.7–5.3 cm. long; the tube 3.1–4.5 cm. long and 5–8 mm. broad at the apex, crimson, narrowly constricted in the basal half; lobes 5–10 mm. long and 3–4.5 mm. broad, greenish-yellow, spreading, narrowly oblong-ovate (ovate-lanceolate or ovate), acuminate or cuspidate-acuminate. Stamens inserted on the

corolla tube about 2/5 of the way from the base to the apex; filaments 1.8–3.1 cm. long equalling or slightly exceeding the corolla tube in mature flowers; anthers 2.5–3 mm. long and 1–2.5 mm. broad, oblong, yellow. Ovary narrowly ovoid; style 3.2–4.6 cm. long, conspicuously exceeding the corolla lobes in mature flowers, exceeding the stamens; stigma peltate, distinctly bilobed. Capsule narrowly ovoid, indistinctly beaked, 11–19 mm. long and 4–6 mm. in diameter, the marcescent corolla persisting until well after the shedding of the seeds. FLOWERING: All year. CHROMOSOME NUMBER: $n = 18$.

DISTRIBUTION: Near sea level to 500 meters along roadsides and in secondary scrub throughout much of British Honduras and into adjacent northeastern Guatemala and northeastern Yucatán, Mexico (MAP 6).

REPRESENTATIVE COLLECTIONS

Mexico. QUINTANA ROO: Chetumal, *Miranda 8116* (MEXU). YUCATAN: Moctezuma, *Enríquez 814* (MEXU). **British Honduras.** BELIZE DIST.: 8 mi. W. of Hattieville on Belize-Cayo road, *Weaver & Wilbur 2255* (A, DUKE). CAYO DIST.: between Mileposts 39 & 40 on Belize-Cayo road, *Weaver & Wilbur 2251* (A, BM, DS, DUKE, F, IJ, LL, MICH, MO, NY, S, UC, US); Mountain Pine Ridge, 9 mi. S. of Georgeville on road to Augustine, *Weaver & Wilbur 2254* (A, BM, DUKE, F, MICH, MO, NY, S, UC, US); Blue Hole Section, Humming Bird Highway, *Gentle 8945* (F, LL); COROZAL DIST.: Corozal-Consijo road, *Lundell 4857* (F, GH, MICH, MO, NY, US). ORANGE WALK DIST.: Honey Camp, *Lundell 538* (BM, DS, F, GH, MO, NY, S, US). STANN CREEK DIST.: Humming Bird Gap, Humming Bird Highway, *Gentle 9246* (F, LL); Freshwater Creek Reserve, *Pelly 16* (BM, F). **Guatemala.** PETÉN: 6.5 km. E. of Dos Lagunas, *Contreras 1617* (LL); Nictun, Lake Petén, *Lundell 3159* (MICH, S); Bajo de Santa Fé, ca. 25 km. E. of Tikál, *Contreras 1438* (F, LL).

Lisianthius axillaris is one of the more distinctive of the *Lisianthius* species. With its crimson corolla tube and solitary flowers in the axils of the foliage leaves, it is not easily mistaken for any other species. The only other species with red flowers is *L. viscidiflorus* (subsect. HERBACEI), of central Guatemala and Chiapas, Mexico. *L. viscidiflorus*, however, has shorter, obtuse corolla lobes, purple anthers, and both terminal and axillary inflorescences of compound dichasia.

Lisianthius francisiae Sprague is synonymous with *L. axillaris*. Sprague, in the description of *L. francisiae*, mentions that the only differences between the two are in the vegetative portion of the plant, *L. francisiae* being herbaceous and freely branched, *L. axillaris* being woody and unbranched; and *L. francisiae* having larger, narrower leaves more narrowed at the base. Leaf shape and size have proved of little taxonomic utility in this genus, both characters varying markedly in different parts of a given plant.

All of the species of sect. LISIANTHIUS subsect. FRUTICOSI are characterized by having a variety of growth forms, and *L. axillaris* is no exception. Freely branched plants and entirely unbranched plants are frequently encountered in this group. The populations of *L. axillaris* which

I have seen in British Honduras were composed of plants with both types of branching patterns (*Weaver & Wilbur 2251* and *Weaver & Wilbur 2254*). The unbranched plants seemed to be those growing in the more unfavorable spots, locations which were either shady or dry.

Lisianthius axillaris is woody only at the base. The type specimen of *L. francisiae*, of which a photograph has been seen, obviously represents the midportion of a single plant. In the midportions, plants of *L. axillaris* are not distinctly woody.

Williams (1968, 1969) included *Lisianthius francisiae* as a synonym of *L. axillaris*. To my knowledge, no author since Sprague has recognized *L. francisiae* as a distinct species.

Lisianthius petenensis Standl. & Steyerm, was based on *Lundell 3153*, from Nictun, Lake Petén, Guatemala (holotype US, isotype MICH). Williams (1968, 1969) considered *L. petenensis* to be a synonym of *L. brevidentatus*. *Lundell 3153*, however, differs strikingly from that species in its much broader, red corolla tube, longer corolla lobes, style not exceeding either the filaments or the corolla lobes, and subsessile leaves. Careful examination of the type and only known collection of *L. petenensis* convinced me that it is a hybrid between two species widely separated from *L. brevidentatus*.

Lisianthius axillaris and *L. saponarioides* are the only species presently known from the Guatemalan department of Petén. Both of these species have been collected in the vicinity of Lake Petén, the type locality of *L. petenensis*. *Lundell 3153* is morphologically intermediate between *L. axillaris* and *L. saponarioides* and is probably a hybrid between them. The putative hybrid and its presumed parents are compared in TABLE 1.

Lundell 3153 is similar to *Lisianthius axillaris* in its red corolla tube, distinctly carinate calyx lobes, and stamens of unequal length in a given flower. It resembles *L. saponarioides* in its inflorescences of frequently sessile, compound dichasia, style not exceeding either the filaments or the corolla lobes, and its indistinctly lobed stigma. In the remaining characters outlined in TABLE 1, it is intermediate between the two species.

In search of further proof of their hybrid origin, pollen was taken from both specimens of *Lundell 3153* and stained with cotton blue-lactophenol. As a control, pollen was taken from a specimen of *Lisianthius axillaris* (*Contreras 1438*, F) and *L. saponarioides* (*Contreras 3766*, F), both from the vicinity of Lake Petén, and similarly stained. The percentage of pollen viability for all four specimens is summarized in TABLE 2.

22. **Lisianthius seemannii** (Griseb.) O. Ktze. Rev. Gen. Pl. 2: 429. 1891 (as *Seemannii*).

Leianthus Seemannii Griseb. in Seemann, Bot. Voy. Herald 170. 1854. TYPE.
Panama. DARIÉN: Piñas, *Seemann 1064* (MO, photo.!; K, holo.).
Lisianthus corymbosus Perk. Bot. Jahrb. 31: 491. 1902. No type designated. Cited specimens presumably at (B) and destroyed during World War II.

Slender subshrubs, glabrous throughout. Stems 0.5–2 m. tall and to

TABLE 1. A morphological comparison of "L. petenensis" and its presumed parents

	L. SAPONARIOIDES	"L. PETENENSIS"	L. AXILLARIS
INFLORESCENCES	Compound dichasia, some nearly sessile	Compound dichasia, some nearly sessile	Solitary, axillary flowers
INFLORESCENCE BRANCHES	Winged	Narrowly winged	Terete
PEDICELS	0–1 mm. long	1–3 mm. long	9–30 mm. long
CALYX	5.5–10 mm. long	7–10 mm. long	8.5–13.5 mm. long
CALYX LOBES	Ridged	Distinctly carinate	Distinctly carinate
COROLLA SHAPE	Salverform, constricted nearly its entire length, lobes flaring	Constricted 2/3 its length, lobes flaring	Tubular-funnelform, constricted 1/2 its length, lobes spreading
COROLLA TUBE	1.0–1.5 cm. long, green	2.3–2.5 cm. long, red	3.1–4.5 cm. long, red
COROLLA LOBES	4–7 mm. long	6–6.5 mm. long	5–10 mm. long
INSERTION OF STAMENS/ LENGTH OF COROLLA TUBE	0.7–0.8	0.6	0.4
FILAMENTS	0.3–0.9 cm. long, equal in length, exceeding the style	1.4–1.6 cm. long, unequal in length, exceeding the style	1.8–3.1 cm. long, unequal in length, not exceeding the style
STYLE	0.6 1.0 cm. long, not exceeding corolla lobes	1.7–2.0 cm. long, not exceeding corolla lobes	3.2–4.6 cm. long, exceeding corolla lobes
STIGMA	Indistinctly lobed	Indistinctly lobed	Distinctly lobed

TABLE 2. **Pollen viability in "L. petenensis" and its presumed parents**

	TOTAL NO. OF GRAINS EXAMINED	% VIABLE	% NOT VIABLE
L. saponarioides	900	97%	3%
"*L. petenensis*"			
Lundell 3153 (US)	1040	19%	81%
Lundell 3153 (MICH)	742	21%	79%
L. axillaris	1209	97%	3%

1.5 cm. in diameter, erect or ascending, terete and gray-brown below, 3–4-angled and green above. Leaves thin-membranaceous, glossy dark green above, paler and dull beneath, the lateral nerves prominent, the blades 1.9–15.7 cm. long and 1.1–5.3 cm. broad, the petioles 0.3–2.5 cm. long or the upper leaves subsessile; principal foliage leaves elliptic, long-acuminate, shortly attenuate into the winged petiole, the leaves on the flowering branches smaller, essentially sessile, lanceolate to ovate, rounded or obtuse at the base. Inflorescences of pedunculate or sessile 1–4-compound dichasia, the lateral branches scorpioid; inflorescence branches contracted and the dichasia or groups of dichasia compacted, 4-angled, 2 of the angles frequently expanded into narrow, scarious wings; flowering branches with several to many pairs of reduced leaves below the first division. Flowers horizontal or nodding, sessile or with pedicels to 6 mm. long. Calyx 8.5–14 mm. long, fused for 1/10–1/6 its length; lobes 7.5–12 mm. long and 1–2 mm. broad, narrowly lanceolate, very long-acuminate, with broad scarious margins, ridged or carinate abaxially. Corolla 3.2–5.2 cm. long, narrowly tubular-funnelform, uniformly lemon-yellow outside and cream-colored inside; tube 2.3–3.7 cm. long and 4–7 mm. in diameter at the apex, constricted in the lower third; lobes (9)10.5–15 mm. long and 2.5–6 mm. broad, widely spreading and slightly recurved at the tips, narrowly lanceolate, long cuspidate-acuminate, ca. half as long as the tube. Stamens inserted on the corolla tube ca. 1/3 of the distance from the base to the apex; filaments 1.9–3.1 cm. long, not surpassing the corolla lobes; anthers 1.5–2.5 mm. long and 1–1.5 mm. broad, oblong, acutish, the connective slightly exserted. Style 2.6–3.7 cm. long, at most equalling the corolla lobes, always surpassing the filaments; stigma peltate. Capsules oblong-ellipsoid, very short-beaked, 9–14 mm. long and 3–6 mm. broad; calyx in fruit equalling or slightly exceeding the capsule; the marcescent corolla persisting until the seeds are shed. FLOWERING: All year. CHROMOSOME NUMBER: $n = 18$.

DISTRIBUTION: From 200–1200 meters, mostly along roadsides, but also in wet or dry secondary scrub or at the margins of forests from north-central Costa Rica, through the mountainous portion of Panama to northwestern Colombia (MAP 7).

REPRESENTATIVE COLLECTIONS

Costa Rica. ALAJUELA: roadside from Alajuela, via San Isidro de Alajuela to Fuente, *Dodge, Thomas & Valerio 4865* (MO); Grecia, road to Sarchí, *Smith 10055* (F, MO). HEREDIA: Sta. Bárbara, au pied du Barba, *Pittier 1670* (US; cited collection of *L. corymbosus*). SAN JOSÉ: vicinity of El General, *Skutch 4109* (GH, MO, S, US); El Rodeo, *Hunnewell 16713* (DUKE, GH). **Panama.** CHIRIQUÍ: between Hato del Jobo and Cerro Vaca, *Pittier 5292* (NY). COCLÉ: Bismarck, above Penonomé, *Williams 259* (NY); 3.5 km. se. of El Valle de Antón along road from El Espino to El Valle, *Weaver 1671* (A, BM, DS, DUKE, F, IJ, LL, MICH, MO, NY, S, UC, US); 2 mi. s. of Coclé, *McDaniel 8248* (DUKE, US). DARIÉN: vicinity of Piñas, *Duke 10637* (MO). HERRERA: 10 mi. s. of Ocú, *Tyson, Dwyer & Blum 2876* (MO); vicinity of Las Minas, La Peña, *Stern, Eyde & Ayensu 1779* (MICH, MO, US). VERAGUAS: Isla de Coiba, *Dwyer 1650* (MO). **Colombia.** ANTIOQUIA: landslide on Río Guapá, 8 km. e. of Guapá, *Haught 4652* (COL, F, US).

Lisianthius seemannii is one of the better collected of the Central American species. With its congested inflorescences, its long narrow calyx and corolla lobes, and its corolla paler inside than out, *L. seemannii* should not be confused with any other species of series *Longifolii*. Its relationships within the group are obscure. It is the only species of series *Longifolii* typically with compound dichasia. It most closely resembles the Jamaican *L. longifolius*, especially vegetatively, but differs strongly from that species in the inflorescence type.

Lisianthius seemannii has the double distinction of being the only species found on a Pacific island (Isla de Coiba), or on the South American continent. *Haught 4652* (COL, F, US) from Dept. Antioquia, Colombia, is the only known collection of a *Lisianthius* species from South America. Ewan determined this specimen as *L. arcuatus* Perk. and reported it (Proc. Biol. Soc. Wash. **63**: 163–166. 1950) as representing a previously unreported extension of the genus into South America. In the same article Ewan stated that *L. seemannii* probably represents the same species as *L. arcuatus*. *L. arcuatus* and *L. seemannii* are certainly not synonymous, the former is rather a synonym of *L. skinneri*. *Haught 4652* undoubtedly is *L. seemannii*.

In the key to the species of *Lisianthius* in Perkins' treatment (1902) of the genus, *L. seemannii* and *L. corymbosus* are separated as follows: *L. seemannii* with ecarinate calyx lobes and the stamens included; *L. corymbosus* with carinate calyx lobes and the stamens shortly exserted. Judging from her treatment in general, by "stamens exserted" Perkins evidently meant that the stamens exceed the corolla lobes when pressed. A duplicate of one of the specimens cited by Perkins as representative of *L. corymbosus*, *Pittier 1670*, is among the collections at the United States National Herbarium. I have seen this specimen and the stamens definitely do not exceed the corolla lobes in any of the flowers. The calyx lobes of *L. seemannii* are never completely ecarinate, although the keel in some specimens is not particularly distinct. At any rate, *Pittier 1670* is so similar in all respects to the type of *L. seemannii*, of which I have

seen a photograph, that a more distinctly carinate calyx would hardly serve to separate *L. corymbosus* as a distinct species.

23. **Lisianthius longifolius** L. Mant. Pl. 43. 1767 (as *Lisianthus*). LECTOTYPE. *T. 9, Figure 1* in P. Browne, Civ. Nat. Hist. Jam. 1756.

Tachia longifolia (L.) Mart. ex G. Don, Gen. Hist. **4:** 197. 1837.
Leianthus longifolius (L.) Griseb. Gen. & Sp. Gent. 196. 1839 [1838].
Leianthus longifolius β *scabridus* Griseb. *loc. cit.* p. 197. TYPE. *Willdenow 3556*, presumably at (B) but not seen.
Lisianthus longifolius var. *scabridus* (Griseb.) Perk. Bot. Jahrb. **31:** 492. 1902.

Spindly subshrubs, minutely puberulous or essentially glabrous. Stems 0.5–2 m. tall and to 2 cm. in diameter, erect, ascending, or sprawling, terete or somewhat quadrate below, green above and gray-brown below, essentially glabrous, or more commonly, moderately to densely short-puberulous above, becoming nearly glabrous below. Leaves firmly membranaceous, glossy grass-green or somewhat gray-green above, paler and dull beneath, glabrous to sparsely short-puberulous above and/or on the midrib below, the margins minutely ciliolate to entire; blades of the foliage leaves (1.5)3–12(14.5) cm. long and (0.5)1–4(5) cm. broad, elliptic to narrowly-elliptic (ovate or lanceolate), short- to rather long-acuminate (acute or rarely obtuse or mucronate), the bases obtuse to cuneate or short-attenuate, the petioles to 2.9 cm. long or the leaves subsessile, glabrous to rather densely short-puberulous; leaves on the flowering branches subsessile or short-petiolate (0.5)1.5–7(8.5) cm. long and (0.3)1–3(4.5) cm. broad, ovate-lanceolate to ovate and lanceolate (elliptic). Inflorescences of dichasia, these often reduced to 1 or 2 flowers; flowering branches with 1–6 pairs of leaves below the first division, sparsely to freely branched, the lower branches usually alternate or bifurcate, each segment diverging from a straight line and appearing almost dichotomous, the upper branches usually opposite, the axes terete, nearly glabrous to rather densely short-puberulous. Flowers subsessile or more commonly pedicellate, the pedicels then to 16 mm. long, relatively stout, glabrous or short-puberulous; bracteoles linear or subulate, scarious. Calyx (0.7)1–2(2.8) cm. long, fused for 1/8–1/10 its length, alate or very rarely merely carinate, when alate the wings 0.5–4 mm. broad, glabrous or sparsely puberulous along the wing or keel; lobes (0.6)0.8–1.8 (2.5) cm. long, lanceolate, long-acuminate, with a scarious or hyaline margin; tube 1–4 mm. long. Corolla (2.9)3.5–6(6.7) cm. long, glutinous, tubular-funnelform; tube (2.3)2.7–3.9 cm. long and 6–14(16.5) mm. broad at the apex, bright yellow, glossy to rather dull, constricted in the lower third; lobes 0.7–2(2.8) cm. long and 3–9 mm. broad, ovate-lanceolate or oblong-lanceolate, abruptly or more or less gradually acuminate, yellow-green, strongly recurved or merely spreading and only the tips recurved, 1/4–3/4 as long as the tube. Stamens inserted on the corolla tube ca. 1/4–1/3 of the distance from the base to the apex; filaments

2–3.8 cm. long, never exceeding the corolla lobes; anthers 2–4.5 mm. long and 1–2 mm. broad, oblong to narrowly oblong, obtuse to acutish at the apex, the connective slightly exserted or not. Style 2.3–4.8 cm. long, very rarely exceeding the corolla lobes, but nearly always conspicuously exceeding the filaments; stigma capitate or somewhat peltate. Capsule ellipsoid or oblong-ellipsoid, beaked, 7–17 mm. long, not including the 1–4 mm. long beak, and 3–7 mm. in diameter; calyx in fruit nearly as long to longer than the capsule; the marcescent corolla persisting until long after the seeds are shed. FLOWERING: All year. CHROMOSOME NUMBER: $n = 18$.

DISTRIBUTION: From sea level to 1500 meters along roadsides and in rather dry secondary scrub throughout Jamaica except for the westernmost parishes (MAP 11).

REPRESENTATIVE COLLECTIONS

Jamaica. CLARENDON: 1.5 mi. se. of Chapelton on road to Suttons, *Weaver & Weaver 1264* (A, DUKE); vicinity of Bog Hole, 1 mi. ne. of Corner Shop, *Weaver & Weaver 1265* (A, DUKE); summit area of Croft's Hill, *Proctor 29266* (IJ); 1 mi. due s. of Arthur's Seat, *Proctor 26443* (IJ, LL, MICH). PORTLAND: 3 mi. e. of Port Antonio, *Weaver & Weaver 941* (A, DUKE, UCWI); near mouth of Rio Grande, *Proctor & Stearn 11860* (IJ). ST. ANDREW: above Gordon Town, *Byndloss 8378* (F, NY); Belleview, near Constant Spring, *Britton 954* (F, NY, US); on road from Kingston to Hardwar Gap, ca. 2 mi. nne. of Irish Town, *Weaver & Weaver 943* (A, DUKE, UCWI, US); 9 mi. se. of Kingston on road to Newstead, *Weaver 1804* (A, DUKE, UCWI, US); road from Chestervale to St. Peters, *Weaver & Weaver 1080* (A, DUKE, IJ). ST. ANN: road from Jamaica A–1 to Hollymount on Mt. Diablo, *Weaver & Weaver 894* (A, DUKE, F, MICH, UCWI, US); between Lime Hall and St. Ann's Bay, *Stearn 718* (A, BM); Roaring River, *Stearn 739* (A, BM). ST. CATHERINE: halfway between Ewarton and Worthy Park, *Adams 13008* (DUKE, UCWI); Bog Walk, *Crawford 819* (GH, NY, US); vicinity of Red Ground, ca. 5.5 mi. n. of Old Harbour, *Weaver & Weaver 1118* (A, BM, DUKE, F, LL, MICH, MO, NY, S, US); 4 mi. sw. of Ewarton on road to Worthy Park, *Weaver & Weaver 1251* (A, BM, DUKE, F, IJ, MICH, MO, UCWI, US); ST. ELIZABETH: hills behind Hampton School, *Weaver & Weaver 1191* (A, BM, DUKE, MICH, MO, UCWI, US); 1.5 mi. ne. of Malvern on road to Leeds, *Weaver & Weaver 1197* (A, DUKE, IJ, MICH, S, US). ST. JAMES: hills overlooking Ironshore Estate, *Proctor 23239* (IJ, LL, MICH, NY); Glen Devon, Montego Bay, *Norman s.n.* (BM). ST. MARY: Gibraltar Beach, near Oracabessa, *Proctor 7455* (IJ). ST. THOMAS: Helen's Gap, Cinchona, *Nichols 64* (F, GH, MO, NY, US); 1–2 mi. nnw. of Whitehall, *Proctor 19805* (A, IJ); ca. 3 mi. nw. of Trinityville, *Proctor 24396* (IJ, LL); 2.5 mi. nw. of Richmond Vale, *Weaver & Weaver 953* (A, DUKE, MICH, US); Arntully, *Weaver & Weaver 976* (A, DUKE, F, US); 1.5 mi. nw. of Bath on road to Beacon Hill, *Weaver & Weaver 1200* (A, BM, DUKE, UCWI, US); along road from Easington to Llandewey, *Proctor 24227* (IJ). TRELAWNY: 1 mi. se. of Windsor, *Proctor 15646* (BM, IJ); 2–3 mi. N by road from Burnt Hill Crossroads, *Hespenheide 1279* (DUKE, GH, LL, MICH, MO, US); road from Burnt Hill to Barbecue Bottom, *Weaver & Weaver 997* (A, DUKE, F, MICH, UCWI, US).

According to Stearn (1957), Linnaeus had virtually no first-hand ex-

perience with Jamaican plants except for those in Patrick Browne's herbarium, which he purchased in 1758. Savage (1945) does not list a specimen of *Lisianthius longifolius* in his catalogue of the extant portion of the Linnaean Herbarium in London. Therefore, it must be assumed either that Patrick Browne's herbarium did not contain a specimen of this species when it was purchased by Linnaeus, or if a specimen was present, it was lost in the interim. It is entirely possible that Linnaeus based his *Lisianthus* (= *Lisianthius*) *longifolius* on an illustration rather than on an actual specimen. In the original description of this species, Linnaeus (1767, p. 43) cited two figures, one of Patrick Browne (1756, *t. 9, figure 1*) and one of Hans Sloane (Voyage 1: *t. 101, figure 1*. 1707). Therefore, a lectotype must be chosen from the illustrations.

Linnaeus's (1767, p. 43) diagnosis of *Lisianthus* (= *Lisianthius*) *longifolius* consists merely of the phrase, "*Lisianthus foliis lanceolatis.*" In addition, he included polynomials given by Browne (1756, p. 157) and Sloane (Cat. Pl. Jam. 58. 1696) for the same species. Linnaeus's diagnosis was obviously made with Browne's polynomial, "*Lisianthus* [*Lisianthius*] *erectus, foliis lanceolatis, floribus singularibus terminalibus*," in mind. In addition, Browne's figure more accurately portrays *L. longifolius* than does Sloane's figure. Therefore, Browne's figure (Civ. Nat. Hist. Jam. *t. 9, figure 1*. 1756) is designated the lectotype of *L. longifolius* L.

Lisianthius longifolius, a rather weedy plant, is found most commonly on roadside banks and in the secondary scrub that covers much of Jamaica. It is frequently encountered and its large, yellow flowers are quite conspicuous. Indeed, *L. longifolius* has been by far the most frequently collected of the species.

Lisianthius longifolius is also the most variable of the species. The characters in which this variation is most pronounced are as follows: (1) pubescence; (2) length of the corolla; (3) length of the calyx; (4) the ratio between the length of corolla lobes and length of corolla tube; and (5) width of the calyx wing. Both the range and the pattern of the variation are most perplexing. These vary independently and abruptly without any obvious correlation with elevation, habitat, or geography. As a result a given population may differ noticeably in certain of these critical characters from another only a few miles away, while closely resembling in these same characters yet another population far removed geographically but differing in others. An analysis of the variation is presented in FIGURE 8.

Eight populations which display the range of variation within the species were scored for each of these critical variables. The degree of pubescence in each population was ranked on a scale from 0 to 4 and represented schematically by means of proportionately filled circles. The empty circles represent the most nearly glabrous type (0); the completely filled circles represent the type which is most densely pubescent (4). The ranges of the remaining characters were numerically evaluated and the values placed proportionately on each of the four axes of a tetragon. The eight populations are:

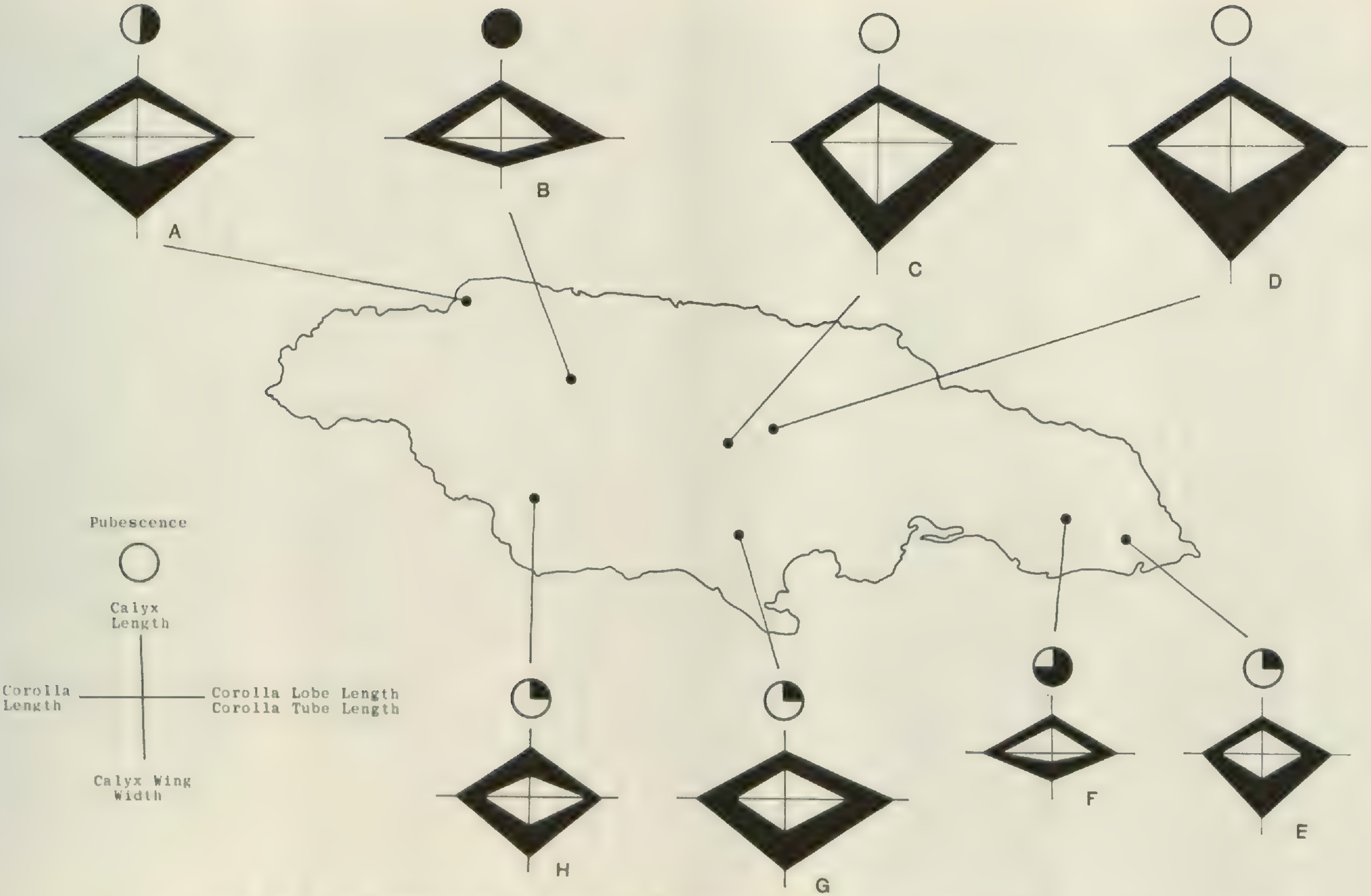

FIGURE 8. An analysis of the variation in *Lisianthius longifolius*. See text for explanation.

A. *Proctor 23239*. ST. JAMES: hills overlooking Ironshore Estate.
B. *Weaver & Weaver 997*. TRELAWNY: road from Burnt Hill to Barbecue Bottom.
C. *Adams 13008*. ST. CATHERINE: half-way between Ewarton and Worthy Park.
D. *Weaver & Weaver 894*. ST. ANN: road from Jamaica A–1 to Hollymount on Mt. Diablo.
E. *Weaver & Weaver 1200*. ST. THOMAS: road from Bath to Beacon Hill.
F. *Weaver & Weaver 976*. ST. THOMAS: Arntully.
G. *Weaver & Weaver 1118*. ST. CATHERINE: vicinity of Red Ground.
H. *Weaver & Weaver 1191*. ST. ELIZABETH: hills behind Hampton School.

Populations D and F are strikingly different; D is glabrous and F is quite densely pubescent and the other characters do not overlap at all. Population E is similar to Population F in length of corolla, length of calyx, and corolla lobes/corolla tube ratio, but is only slightly pubescent and the width of the calyx wing is much broader, the range of variation of which overlaps that of Population D. Population C is similar to Population D, but the corolla and calyx are both slightly shorter in the former. Population B is similar to Population C in all respects except that the wing on the calyx is much narrower and the plants are densely pubescent; it is intermediate between Populations C and F. Population A resembles Population B except that it is less densely pubescent and the calyx wing is broader, and it is therefore intermediate between that population and Population C. Population H resembles Population E, from the other end of the island, except that it is slightly larger in all respects. Population G is intermediate between Populations C and H.

Both Grisebach (1839, 1845) and Perkins (1902) recognized a variety *scabridus* of *Lisianthius* (or *Leianthus*) *longifolius*. No authentic material of this has been seen, but *ex char*. it would seem to be something resembling Populations E or F above. With such a striking array of intermediate and overlapping forms, it is impossible to segregate any of these populations, or the groups of populations of which they are typical, as a distinct taxon of any rank.

In his *Flora of the British West Indian Islands*, Grisebach (1862), instead of recognizing var. *scabridus* as before, described a new variety, *gracilis*, of *Leianthus* (= *Lisianthius*) *longifolius*. At the same time he described the range of *L. longifolius* as including Cuba. No authentic material of his var. *gracilis* has been seen, but the description could apply equally well to some specimens of *Lisianthius longifolius* as here interpreted or to the Cuban *L. glandulosus*. Since the name cannot be correctly applied at present, it is here considered a *nomen dubium*.

24. **Lisianthius cordifolius** L. Mant. Pl. 1: 43. 1767 (as *Lisianthus*).
✓TYPE. Specimen no. 213.1 (Savage, 1945) in the Linnaean Herbarium (LINN), probably collected by P. Browne. (Microfiche (IDC 5075. 18: II. 1.) seen.)

Tachia cordifolia (L.) Mart. ex G. Don, Gen. Hist. 4: 197. 1837.

Leianthus cordifolius (L.) Griseb. Gen. & Sp. Gent. 197. 1839 [1838].
Leianthus longifolius γ *cordifolius* (L.) Griseb. Fl. Brit. W. Ind. Isl. 424. 1862.
Lisianthus longifolius var. *cordifolius* (L.) Perk. Bot. Jahrb. 31: 492. 1902.

Low subshrubs, moderately to densely puberulous. Stems 3–6 dm. tall and to 1 cm. in diameter, erect or ascending, greenish or straw-colored above and gray-brown below, the branches nearly always alternate, moderately to densely short-puberulous above, becoming nearly glabrous below. Leaves firmly membranaceous, dull-textured, bright green above, paler and dull beneath, the midribs short-puberulous (glabrous), the margins minutely ciliolate or rarely entire; blades of the foliage leaves 1.2–4.9 cm. long and 0.6–2 cm. broad, gradually acuminate, the base attenuate to obtuse and rounded or subcordate, the petioles densely short-puberulous, winged, 1.5–7 mm. long; leaves on the flowering branches decreasing in size toward the apex, 0.3–2.2 cm. long and 0.2–1.5 cm. broad, the lower ones narrowly ovate, rounded or subcordate at the base and short-petiolate, the upper ones broadly ovate, distinctly cordate at the base and subsessile. Inflorescences of apparently simple dichasia, these reduced to 1 or 2 flowers, or very rarely 3-flowered; flowering branches with several to many pairs of leaves between each division of the primary and secondary axes, often unbranched and terminated by 1 to 2 flowers, or sparsely to freely branched, the branching bifurcate or very rarely opposite, the axes terete, moderately to densely short-puberulous. Flowers nodding, the pedicels relatively slender, short-puberulous, 3–10 mm. long; bracteoles subulate, scarious. Calyx 7–11 mm. long, fused for 1/8–1/5 its length; lobes 6–9.5 mm. long and 1–2 mm. broad, lanceolate, long-acuminate, carinate abaxially, with broad scarious or hyaline margins, the central green band ca. 1/2 the total width of the lobe; tube 1–2 mm. long, sometimes sparsely puberulous at the base. Corolla tubular-funnelform, 3.0–4.4 cm. long; the tube 2.1–3.2 cm. long and 6–8 mm. in diameter at the apex, bright yellow, constricted in the lower third; lobes 9–13.5 mm. long and 3.5–9.5 mm. broad, 1/3–4/10 as long as the tube, spreading and the tips recurved, yellow-green, narrowly ovate to ovate-lanceolate. Stamens inserted on the corolla tube ca. 1/3 of the distance from the base to the apex; filaments 1.9–3.3 cm. long, the longest ones nearly equalling or barely surpassing the corolla lobes; anthers 2–2.5 mm. long and 1–1.5 mm. broad, oblong, obtuse or acutish at the apex, the connective slightly exserted. Style 2.4–3.8 cm. long, exceeding (equalling) the corolla lobes, always exceeding the filaments; stigma capitate. Capsule ellipsoid or oblong-ellipsoid, short-beaked, 9–12 mm. long, not including the 1–2 mm. long beak, and 3–6 mm. in diameter; calyx in fruit 2/3 as long to longer than the capsule; the marcescent corolla persisting long after the seeds are shed. FLOWERING: Nov.–June. CHROMOSOME NUMBER: $n = 18$.

DISTRIBUTION: From 70 to 400 meters in crevices of rock of steep limestone gorges, or rarely in dry scrubby forest on limestone in the vicinity of Kingston, Jamaica (MAP 12).

REPRESENTATIVE COLLECTIONS

Jamaica. ST. ANDREW: gorge of the Cane River, below the falls at Newstead, *Weaver 1821* (A, DUKE, F, MICH, UCWI, US); Cane River Valley, *Harris 12315* (A, F, MO, NY, S, US); on canyon wall along Hope River, *Yuncker 17374* (F, MICH, S); Hope River Gorge, *Norman 171* (BM); Long Mountain, back of Kingston, *Webster & Wilson 4860* (A, IJ, MICH, S, US).

Lisianthius cordifolius is one of the most restricted of the species, known from only two limestone gorges and an adjacent mountain in southeastern Jamaica. It is closely related to *L. longifolius*, and in fact, has been considered to be a variety of that species by Grisebach (1862) and Perkins (1902). *L. cordifolius* differs from *L. longifolius* in its carinate calyx lobes, its branching very rarely opposite, its flowering-branch leaves cordate at the base, and its styles equalling or surpassing the corolla lobes. As explained earlier, *L. longifolius* is a bewilderingly variable species, and some specimens approach *L. cordifolius* in their morphology. However, no specimens have been seen which are not immediately referable to one species or the other.

There is some indication that *Lisianthius cordifolius* and *L. longifolius* may hybridize in nature. *L. cordifolius* is known from only three populations in an eight square mile area in the vicinity of Kingston, Jamaica. Although apparently not common, *L. longifolius* has been collected in that same area. It appears that the pollen viability of one of the three populations of *L. cordifolius*, *Webster & Wilson 4860*, is somewhat lower than might be expected in a fully differentiated, fertile species, giving rise to the possibility of its being a hybrid. The habitat of this population, however, is quite different from that of the other two known populations of *L. cordifolius*. *Webster & Wilson 4860* was collected in dry, scrubby forest on limestone, while the other two populations grew in rock crevices of steep limestone cliffs. The reduced pollen viability of *Webster & Wilson 4860* was discovered near the end of my study when field and experimental work was no longer possible. Thus, whether this reduced pollen viability is due to an unfavorable environment or to the population being a hybrid one, I cannot determine at present.

Experimental crosses have been carried out between plants of *Lisianthius cordifolius* and *L. longifolius* grown in the greenhouse of Duke University. The flowers of the seed plants were emasculated before the anthers had dehisced and the plants were isolated in a separate chamber of the greenhouse. All unused flowers were removed before anthesis as a preventative against stray pollen. Pollination was accomplished by rubbing an anther from the pollen parent across the stigmas of the seed parents until the stigmas were covered with pollen. The pollination procedure was repeated every day until the flowers withered. The results are summarized in TABLE 3.

The seed set in the hybrid cross (Cross 2) is somewhat reduced from that obtained when the seed parent (*L. cordifolius*, Cross 3) was selfed. The hybrid seeds were planted and the germination was high. The seedlings are vigorous but to date have not flowered. Therefore the presence

TABLE 3. **Summary of experimental crosses between Lisianthius cordifolius and L. longifolius**

CROSS NO.	POLLEN PARENT	SEED PARENT	TOTAL NO. OF FLOWERS	TOTAL NO. OF SEEDS	AV. NO. OF SEEDS
1	*L. longifolius (Weaver 2344)*	*L. longifolius (Weaver 2344)*	10	2515	251.5
2	*L. longifolius (Weaver 2344)*	*L. cordifolius (Weaver 2343)*	45	11274	250.4
3	*L. cordifolius (Weaver 2343)*	*L. cordifolius (Weaver 2343)*	9	3455	383.9

or absence of an effective barrier to hybridization, resulting in reduced pollen or ovule viability, between these two species cannot now be determined.

Extensive field and experimental work must be done before the relationship between *Lisianthius cordifolius* and *L. longifolius* can be explained. However, the morphological evidence stongly suggests that they are distinct taxa. Since the taxa are rather closely sympatric, with obvious intermediates absent, I prefer to treat them as distinct species.

b. **Lisianthius** sect. **Lisianthius** subsect. **Fruticosi** ser. **Exserti** Weaver, *ser. nov.*

Frutices vel arbusculae graciles, omnino glabrae. Styli filamenta staminumque longissimi exserta, segmentis exsertis corolla longior. Pollinis grana exinio laevi vel fere laevi. SPECIES TYPICA: L. *exsertus* Sw.

50053792

25. **Lisianthius exsertus** Sw. Prodr. 40. 1788; Fl. Ind. Occ. 1: 346. 1797 (as *Lisianthus*). LECTOTYPE. **Jamaica,** without exact locality, *Swartz* (s!).

Leianthus exsertus (Sw.) Griseb. Gen. & Sp. Gent. 197. 1839 [1838].
Lisianthus callosus Bertero in Spreng. Syst. **1:** 585. 1825 [1824].
Tachia swartzii G. Don, Gen. Hist. **4:** 197. 1837, *nom. illegit.* (Art. 63. I.C.B.N.).

Slender shrubs, rarely becoming treelike, glabrous throughout. Stems 1–6 m. tall and to 6 cm. in diameter at the base, erect or ascending, gray-brown at the base and green above, terete, brittle, distinctly woody. Leaves membranaceous, glossy bright green above, paler and dull beneath, the principal lateral veins evident but often not conspicuous, the blades 3–13.4 cm. long and 1–5.5 cm. broad, elliptic or elliptic-oblong, with a tendency to be widest slightly above the middle, gradually short acuminate or rarely acute, the bases sometimes unequal, attenuate into the 0.5–2.6 cm. long petiole. Inflorescences of pedunculate, apparently simple dichasia; flowering branches once or twice ternately divided, each division terminated by a dichasium; stalks of the flowering branches ascending, flat-

tened in cross section; dichasial branches terete. Flowers nodding, the pedicels 6–11 mm. long; bracteoles subulate, scarious. Calyx 5–11 mm. long, fused for ca. 1/4 its length; lobes 5–8.5 mm. long and 1–1.5 mm. broad, lanceolate or subulate-lanceolate, short-acuminate, mostly scarious but with a narrow green band in the center, slightly ridged abaxially; tube 1–2.5 mm. long. Corolla tubular-campanulate, 2–3.3 cm. long; tube 1–1.6 cm. long and 4–8 mm. in diameter at the widest point, yellow, constricted for about half its length; lobes 2.5–5.5 mm. long and 2–4.5 mm. broad, nearly as broad as long, 1/6–1/9 as long as the tube, yellow-green, erect or slightly spreading, broadly triangular-ovate, abruptly short-acuminate. Stamens inserted just below the middle of the corolla tube; filaments 3.5–6.6 cm. long, greatly exserted, exceeding the corolla lobes by 2.5–5 cm.; the longest one usually equalling or surpassing the style; anthers 2.5–3.5 mm. long and ca. 1 mm. broad, narrowly oblong, narrowed at the apex, the connective slightly exserted. Styles 3.4–6.7 cm. long, greatly exserted; stigma peltate. Capsule oblong-ellipsoid, long-beaked, 9–14 mm. long, not including the 2.5–5 mm. long beak, and 3–5 mm. in diameter; the marcescent corolla not persisting until the seeds are shed. FLOWERING: All year. CHROMOSOME NUMBER: $n = 18$.

DISTRIBUTION: From 300 to 1100 meters in secondary thickets or scrub, or along roadsides, or rarely in elfin woodland, in the eastern and central parishes of Jamaica (MAP 12).

REPRESENTATIVE COLLECTIONS

Jamaica: without locality, *Swartz* (BM, S; isolectotypes). ST. ANDREW: vicinity of Cooper's Hill, Red Hills, *Proctor 18262* (A, IJ); vicinity of Brandon Hill, *Proctor 23499* (IJ, LL); Moresham River, west side, 1/4 mi. above Hermitage Dam Reservoir, *Stearn 410* (A, BM, S). ST. CATHERINE: Grandodiorite District, ca. 1 mi. sw. of Parks Road, *Webster & Wilson 1954* (IJ, MICH, US). ST. MARY: ne. slopes of Cum See Hill, above Longroad P.O., *Proctor 22629* (IJ). CLARENDON: Mason River Savannah, *Crosby & Anderson 1151* (DUKE, MICH); Peckham Woods, *Harris 11099* (NY, US). PORTLAND: 100–200 m. w. of Silver Hill Gap, along road from Section to Silver Hill Gap. *Weaver & Weaver 951* (A, DUKE, UCWI); Proctor's Pool, *Adams 9151* (DUKE); trail n. & w. of Silver Hill Gap, *Hespenheide 773* (DUKE, GH, LL, MICH); east slope of the John Crow Mountains, 1.5–2.5 mi. sw. of Ecclesdown, *Proctor 22114* (IJ, MICH).

Swartz's herbarium presently at Stockholm (S), includes three specimens of *Lisianthius exsertus*, two with the inscription "Jamaica" and one with "Ind. occ." There is also a Swartz specimen of the same species, with the inscription "Jamaica," among the collections at the British Museum (BM). The more complete of the two inscribed "Jamaica" at Stockholm best demonstrates the characters described by Swartz and is here designated the lectotype of *L. exsertus* Sw.

Although I have seen neither the type nor any other authentic material of *Lisianthus callosus* Bertero, the original description suggests very strongly that the plant is the same as *L. exsertus*. This description is re-

produced below in its entirety (from Bertero in Spreng. Syst. 1: 585. 1825).

callosus Berter. 2. L. foliis basi inaequalibus acutis, petiolis calloso annulo ramos amplectentibus, pedunculis corymbosis, staminibus longissimis. *Jamaica.* (Flores ochroleuci.)

This diagnosis fits very well the description of *Lisianthius exsertus* and excludes all other known Jamaican species. The only other species with stamens that could possibly be described as "longissimis" is *L. capitatus*, but that species has subcapitate inflorescences. The primary difference between the diagnosis of *L. callosus* and that of *L. exsertus*, immediately above it in Sprengel's treatment, is the phrase ". . . *petiolis calloso annulo ramos amplectentibus* . . ." The epithet "*callosus*" obviously refers to this character, which rather than being diagnostic for any single species, would describe equally well every species in the genus.

George Don (1837) cited the earlier *Lisianthius exsertus* Sw. as a synonym of his *Tachia swartzii*, the specific epithet of the latter therefore illegitimate (Art. 63, I.C.B.N.). He included two other species of *Lisianthius* in *Tachia* [*T. longifolia* (L.) Mart. = *L. longifolius* L. and *T. cordifolia* (L.) Mart. = *L. cordifolius* L.] but did not change their epithets.

c. **Lisianthius** sect. **Lisianthius** subsect. **Fruticosi** ser. **Umbellati** Weaver, *ser. nov.*

Frutices vel arbores graciles, omnino glabri. Folia oblanceolata vel anguste obovata. Inflorescentiae axillares, dense compactae, capitula vel umbellas simulantes, paribus duobus bractearum involucratarum. Styli filamentaque longe exserta. Pollinis grana exinio reticulato. SPECIES TYPICA: *L. umbellatus* Sw.

KEY TO THE SPECIES OF SERIES UMBELLATI

Pedicels in fruit 8–20 mm. long; corolla tubular, the tube 2.2–3.1 cm. long and 4–6 mm. in diameter at the broadest point, the lobes abruptly short-acuminate, 2–3.5 mm. long and 2–3 mm. broad, about as broad as long, 1/8–1/10 as long as the tube; filaments exceeding the corolla lobes by no more than 8 mm.; styles exceeding the corolla lobes by no more than 1.5 cm.; calyx 4.5–7 mm. long, the lobes 2–4.5 mm. long. . . . . 26. *L. umbellatus.*

Pedicels in fruit to 7.5 mm. long, or the fruits sessile; corolla tubular-campanulate, the tube 1.5–2.3 cm. long and 7.5–10 mm. in diameter at the broadest point, the lobes acute to obtuse, 4.5–7.5 mm. long and 3.5–6 mm. broad, 1/4–1/3 as long as the tube; filaments exceeding the corolla lobes by 8–20

mm.; style exceeding the corolla lobes by 1.1–3.4 cm.; calyx 6.5–12.5 mm. long, the lobes 4–8.5 mm. long. ..... *27. L. capitatus.*

26. **Lisianthius umbellatus** Sw. Prodr. 40. 1788; Fl. Ind. Occ. 1: 350. 1797 (as *Lisianthus*). LECTOTYPE. **Jamaica,** without exact locality, *Swartz* (S!).

Leianthus umbellatus (Sw.) Griseb. Gen. & Sp. Gent. 199. 1839 [1838].

Glabrous, spindly, unbranched or sparsely branched shrubs, often becoming treelike. Stems erect or ascending, 1.5–6 m. tall and to 6 cm. in diameter, brittle, gray-brown below and green above, terete. Leaves firmly membranaceous or subcoriaceous, grass-green and glossy above, paler and dull beneath, the blades (7)10–29 cm. long and (2)3–9.5 cm. broad, oblanceolate to narrowly obovate (elliptic), abruptly or gradually short-acuminate, the bases long-attenuate into the 1.1–4.1 cm. long petiole. Inflorescences appearing umbellate, the primary and secondary axes greatly contracted, closely subtended by 2 pairs of opposite, decussate, leafy bracts, the outer pair broadly ovate or suborbicular, rounded or broadly cuneate at the base, 1.8–7.5 cm. long and 1.5–5 cm. broad, the inner pair narrower, elliptic or tending toward oblanceolate, more attenuate at the base, 2–6.2 cm. long and 0.7–2.4 cm. broad; the stalks ascending, flattened in cross section, 7.2–19.4 cm. long. Flowers ascending or horizontal, pedicellate. Calyx pale green, and subscarious, fused for 1/3–1/2 its length; lobes 2–4.5 mm. long and 1–1.5 mm. broad, lanceolate or subulate, acuminate, ecarinate; tube 2–2.5 mm. long. Corolla tubular, 2.5–3.4 cm. long; tube bright yellow, constricted in the lower half, somewhat inflated and widest below the apex; lobes yellow-green, erect or slightly spreading, orbicular, abruptly short-acuminate. Stamens inserted just below the middle of the corolla tube; filaments 1.7–2.9 cm. long, well exserted; anthers 2–3.5 mm. long and ca. 1 mm. broad, more than twice as long as broad, narrowly oblong, narrowed at the apex, the connective slightly exserted. Style 2.7–3.7 cm. long, well exserted, always exceeding the filaments, exceeding the corolla lobes by up to 1.5 cm.; stigma peltate. Capsule oblong-ellipsoid, long beaked, 1.0–1.5 cm. long, not including the 1.5–2.5 mm. long beak, and 3–5 mm. in diameter; the marcescent corolla not persisting until the seeds are shed. FLOWERING: Feb.–Apr. CHROMOSOME NUMBER: $n = 18$.

DISTRIBUTION: In wet limestone thickets at ca. 600 meters; known from 2 localities, on Dolphin Head Mountain and at the edges of the Cockpit Country in northwestern Jamaica (MAP 13).

REPRESENTATIVE COLLECTIONS

Jamaica: near Troy, *Perkins 1321* (GH). HANOVER: summit of Dolphin Head Mountain, near the village of Askenish, *Weaver 1832* (A, BM, DUKE, F, MO, UCWI, US); slopes of Dolphin Head Mountain, *Harris 10292* (F, NY, US).

Swartz did not designate a type specimen of *Lisianthius umbellatus.* His herbarium, now at Stockholm (S), includes three specimens of this

species, two inscribed "Jamaica" and one inscribed "Ind. occ." The more complete of the former is designated lectotype of *L. umbellatus* Sw.

Several authors before 1909 included under *Lisianthius umbellatus* plants now referred to *L. capitatus*. Grisebach (1862) gave the distribution of *L. umbellatus* as "in high mountains Portland, Guy's Hill s. Anns, Dolphin westmoreland." Similarly, Perkins (1902) cited specimens as typical of *L. umbellatus* from both eastern and western Jamaica, including *Harris 6683*, from St. Ann, which was later cited by Urban in the original description of *L. capitatus*.

Although in rather poor condition, the lectotype specimen of *Lisianthius umbellatus*, with its long pedicels, short calyx, and short, orbicular corolla lobes clearly resembles the plants presently known only from Dolphin Head Mountain in Hanover Parish and from near Troy at the edge of the Cockpit Country in western Jamaica.

27. **Lisianthius capitatus** Urb. Symb. Antill. **6**: 33. 1909 (as *Lisianthus*). LECTOTYPE. **Jamaica.** ST. ANN: Hollymount, near Ewarton, *Harris 8878* (BM!).

Glabrous, spindly, unbranched or sparsely branched shrubs, often becoming treelike. Stems erect or ascending, 1.5–6 m. tall and to 7 cm. in diameter, gray-brown below and green above, terete, brittle. Leaves firmly membranaceous or subcoriaceous, dark glossy green above and paler beneath, the blades (6)12–31 cm. long and (1.5)3.5–6.5 cm. broad, oblanceolate (elliptic), abruptly or gradually short-acuminate, the bases long-attenuate into the 0.7–3.7 cm. long petiole. Inflorescences appearing capitate or umbellate, primary and secondary axes contracted, closely subtended by 2 pairs of opposite, decussate, foliaceous bracts, these elliptic or ovate, rarely orbicular, broadly attenuate or rarely rounded at the base, the outer pair 1.9–8.3 cm. long and 1.5–7.1 cm. broad, the inner pair smaller and narrower, 1.5–7.1 cm. long and 0.4–3.6 cm. broad; stalks ascending, flattened in cross-section, 7.0–23 cm. long. Flowers erect, sessile or short-pedicellate. Calyx pale green and subscarious, fused for 1/3–1/2 its length; lobes 4–8.5 mm. long and 1–2 mm. broad, lanceolate or subulate, long-acuminate, ecarinate; tube 2.5–4 mm. long. Corolla tubular-campanulate, 1.8–2.8 cm. long; tube yellow or yellow-green, constricted to slightly above the middle; lobes yellow-green, erect or slightly spreading, broadly ovate or rarely suborbicular, the apices obtuse or more rarely acute. Stamens inserted just above the middle of the corolla tube; filaments 1.9–3.2 cm. long, greatly exserted; anthers 3.5–4.5 mm. long and ca. 1 mm. broad, more than 3 times longer than broad, narrowly oblong, narrowed at the apex, the connective slightly exserted. Style 2.7–5 cm. long, greatly exserted, surpassing the corolla lobes by 1.1–3.4 cm., always exceeding the filaments; stigma peltate. Capsule oblong-ellipsoid, long-beaked, 10–17 mm. long, not including the 2–3.5 mm. long beak, and 3–8 mm. in diameter; the marcescent corolla not persisting until the the seeds are shed. FLOWERING: Jan.–Sept. CHROMOSOME NUMBER: $n = 18$.

DISTRIBUTION: From sea level to 800 meters, at edges of forests and in moist thickets on limestone, rarely on rocky headlands by the sea, in the eastern and central parishes of Jamaica, principally in the John Crow Mountains, the Mt. Diablo Massif, and the Cockpit Country (MAP 13).

REPRESENTATIVE COLLECTIONS

Jamaica. PORTLAND: vicinity of Blue Hole, *Weaver & Weaver 940* (A, DUKE, F, UCWI); John Crow Mountains, east slope, 1.5 mi. w. of Ecclesdown, *Webster & Wilson 5134* (A, MICH). ST. ANDREW: 0.8 mi. e. of Rock Hall on road to Park Road, *Weaver & Weaver 1291* (A, DUKE, UCWI, US). ST. ANN: prope Moneague ad Guy's Hill, *Alexander* (NY, cited collection); Hollymount, near Ewarton, *Harris 8878* (F, NY; isolectotypes); road from Jamaica A–1 to Hollymount on Mt. Diablo, *Weaver & Weaver 983* (A, BM, DUKE, F, IJ, LL, MICH, MO, NY, S, UC, US). ST. THOMAS: John Crow Mountains, Big Level Area, *Webster & Proctor 5524* (A, IJ, MICH, US). TRELAWNY: Cockpit Country, road from Burnt Hill to Barbecue Bottom, *Weaver & Weaver 1002* (A, BM, DUKE, F, LL, MICH, MO, NY, S, UCWI, US); vicinity of Ramgoat Cave, Cockpit Country, *Howard, Proctor & Stearn 14684* (BM, IJ).

Although not described until 1909, *Lisianthius capitatus* has been part of various collections made since the middle of the 19th century that were determined as *L. umbellatus*. It is by far the more common of the two species in series *Umbellati*. Judging from the determination of some of the more recent collections, it is apparent that the species are still sometimes confused. Vegetatively *L. capitatus* is very similar to *L. umbellatus*. However, the flowers of the two species are strikingly different. As pointed out by Urban in the original description of *L. capitatus*, that species differs from *L. umbellatus*: in its flowers sessile or short-pedicellate; its longer calyx; its shorter and much broader corolla; its corolla lobes acute or obtuse, longer than broad, longer in absolute length and much longer in relation to the tube; and in its more greatly exserted styles and filaments.

Urban, in describing *Lisianthius capitatus* cited three specimens as representative of his new species. These, which are syntypes, are: *Harris 8878* and *Harris 6683*, from Hollymount on Mt. Diablo, and *Alexander s.n.*, "prope Moneague ad Guy's Hill." All of Urban's original material [except for some Ekman specimens at Stockholm (S)] was destroyed during the bombing of Berlin in World War II (H. Scholz, *in litt.*). Several duplicates of the above-mentioned specimens have been seen. Of these, the specimen of *Harris 8878* at the British Museum is the best preserved and best exhibits the characters described by Urban. This specimen is entirely typical of those from the Mt. Diablo area and undoubtedly represents the taxon described by Urban. Therefore, *Harris 8878* (BM) is designated the lectotype of *L. capitatus* Urb.

SPECIES NON SATIS NOTA

1. **Lisianthius calciphilus** Standl. & Steyerm., Fieldiana Bot. 22: 267. 1940 (as *Lisianthus*). TYPE. **Guatemala.** ALTA VERAPAZ: Finca Los Alpes, *Wilson 356* (F!).

Low shrubs (?), glabrous throughout. Stems terete below and 4-angled above. Leaves firmly membranaceous, papillose above and on the margins, subsessile or short-petiolate, narrowly ovate, the apices acuminate, the bases cuneate or rounded. Inflorescences of compound dichasia, but the terminal flower aborted and the lateral branches then appearing to be complete dichasia; branches of the inflorescence strongly 4-angled, the angles expanded into narrow, scarious wings. Bracteoles oblanceolate, green at least along the midline, to 8 mm. long. Calyx ca. 7 mm. long; lobes ca. 5 mm. long, lanceolate, long-acuminate, scarious margined, carinate abaxially. Corolla tubular-funnelform, 3.6–3.9 cm. long, yellow; lobes ca. 6 mm. long and 3 mm. broad, 1/5 as long as the tube, spreading, ovate-lanceolate, abruptly short-acuminate. Filaments 2.2–2.6 cm. long, not exceeding the corolla lobes; anthers broadly oblong, obtuse. Style 2.9–3.4 cm. long, exceeding the corolla lobes; stigma peltate. Capsules not seen.

Lisianthius calciphilus is definitely referable to the typical section of *Lisianthius* as here interpreted. Only the type specimen is known, and it cannot be placed in any of the species recognized in this study. Therefore, *L. calciphilus* is very possibly a good species. The type specimen, *Wilson 356* from Dept. Alta Verapaz, Guatemala, consists of two flowering shoots. However, it is impossible to determine whether these shoots represent primary or secondary (lateral) axes. They are determinate, but not monopodial, and the branching is not excurrent. Therefore, if these shoots represent primary axes, the plant would not fit into either subsect. HERBACEI or subsect. FRUTICOSI, but would rather appear to be somewhat intermediate between them. If the shoots represent lateral axes, they would be similar to the flowering branches of certain species, particularly *L. longifolius* or *L. seemannii*, of subsect. FRUTICOSI, series *Longifolii*.

In the original description of *Lisianthius calciphilus*, Standley and Steyermark suggest that their new plant is close to *L. collinus*. (= *L. brevidentatus* var. *collinus*, subsect. HERBACEI). From that plant *L. calciphilus* differs in its longer corolla lobes, broader corolla tube, and much larger bracteoles. Williams (1968, 1969) also associated *L. calciphilus* with *L. collinus*, reducing both to synonymy under *L. brevidentatus*. In several respects, *e.g.* flower form, papillose leaves, and subfoliaceous bracteoles. *Wilson 356* closely resembles *L. acuminatus*. However if the structures preserved are indeed lateral flowering branches, they are much more greatly proliferated than in that species and would more closely resemble those of *L. longifolius* or *L. seemannii*.

It seemed possible that *Wilson 356* might be a hybrid between *L. acuminatus* and a species in subsect. HERBACEI, perhaps *L. quichensis* or *L. brevidentatus*. thus possibly explaining its peculiar inflorescences. However, its pollen showed nearly 100 percent stainability in cotton blue-lactophenol.

Until more material is available, or until I have studied it in the field, I cannot place *Lisianthius calciphilus* with any degree of confidence in my classification of the species of *Lisianthius* and therefore must treat it as a ***species non satis nota***.

EXCLUDED NAMES

Lisianthus acuminatus Desr. in Lam. Encycl. 3: 660. 1804. TYPE. **Guadeloupe:** *de Badier* (P) (Microfiche, IDC 6207. 446: II. 7!) = *L. frigidus* Sw. *fide* Grisebach (1839) = **Calolisianthus frigidus** (Sw.) Gilg.

Lisianthus acutangulus Mart. Flora **21** (2-Beibl.): 49. 1838. TYPE: *Martius 216* (M) = **Calolisianthus acutangulus** (Mart.) Gilg in Engler & Prantl, Nat. Pflanzenfam. **4**(2): 101. 1895.

Lisianthus acutangulus Ruiz & Pav. Fl. Peruv. **2:** 14. *t. 122, figure a.* 1799. TYPE: "In *Panatahuarum* montibus ad *Chinchao* runcationes in locis meridionalibus," *Ruiz & Pavon* (MA) = **Chelonanthus alatus** (Aubl.) Pulle *fide* Williams (1968).

Lisianthus acutilobus Steyerm. Bol. Soc. Venez. Cienc. Nat. **26:** 439. *figure 9.* 1966. TYPE: *Steyermark & Nilsson 732* (VEN); referable to **Pagaea** Griseb.

Lisyanthus alatus Aubl. Hist. Pl. Guiane **1:** 204; **3:** *t. 80.* 1775. TYPE: "Habitat in locis incultis Caienne & Guiane," *Aublet* (P) (Microfiche, IDC 6213. 23: IV. 6!) = **Chelonanthus alatus** (Aubl.) Pulle, Enum. Vasc. Pl. Surinam 376. 1906.

Lisyanthus alatus Willd. ex Griseb. Gen. & Sp. Gent. 185. 1839 (*nom. nud.*) = *L. trifidus* HBK. *fide* Grisebach (loc. cit.); *ex char.* referable to **Chelonanthus** (Griseb.) Gilg.

Lisianthus albus Spruce ex Prog. in Mart. Fl. Bras. **6**(1): 237. 1866. TYPE: "In vicinis Barra prov. do Alto Amazonas [Brazil]," *Spruce* = **Chelonanthus albus** (Spruce ex Prog.) Badillo in Pittier et al., Cat. Fl. Venezolana **2:** 293. 1947.

Lisianthus alpestris Mart. Nov. Gen. & Sp. **2:** 93. *t. 171.* 1827 = *Helia alpestris* (Mart.) O. Ktze. Rev. Gen. Pl. **2:** 428. 1891. This should be transferred to **Calolisianthus** (Griseb.) Gilg, according to Nilsson (1970).

Lisianthus amoenus Miq. Linnaea **19:** 139. 1847. TYPE: "Crescit in Para superiore juxta sylvam [Brazil]," *Focke* (U?) = *Helia amoena* (Miq.) O. Ktze. Rev. Gen. Pl. **2:** 428. 1891; *ex char.* referable to **Chelonanthus** (Griseb.) Gilg.

Lisianthus amplissimus Mart. Nov. Gen. & Sp. **2:** 96. *t. 175.* 1827 = **Calolisianthus amplissimus** (Mart.) Gilg in Engler & Prantl, Nat. Pflanzenfam. **4**(2): 101. 1895.

Lisianthus angustifolius HBK. Nov. Gen. & Sp. **3:** 181. 1818. TYPE: "In radicibus montis Duidae, prope Esmeraldam [Venezuela]," *Humboldt & Bonpland* (P) (Microfiche, IDC 6209. 72: III. 3!) = **Chelonanthus angustifolius** (HBK.) Gilg in Engler & Prantl, Nat. Pflanzenfam. **4**(2): 98. 1895.

Lisianthus angustifolius Mart. Nov. Gen. & Sp. **2:** 99. *t. 178, figure 1.* 1827 = *L. tenuifolius* Spreng. Syst. Cur. Post. 339. 1827. According to Nilsson (1970) this should be transferred to **Calolisianthus** (Griseb.) Gilg.

Lisianthus anomalus HBK. Nov. Gen. & Sp. **3:** 184. 1818. TYPE: "Crescit in montosis inter Honda et Mariquita Novo-Granatensium," *Humboldt & Bonpland* (P) = **Symbolanthus anomalus** (HBK.) Gilg in Engler & Prantl, Nat. Pflanzenfam. **4**(2): 99. 1895.

Lisianthus aphyllus Vell. Fl. Flum. 2: 78. 1825. From the illustration this is a species of **Voyria** Aubl.

Lisianthus arboreus Spruce ex Prog. in Mart. Fl. Bras. 6(1): 240. *t. 64, figure 1.* 1866. TYPE: *Spruce 3551* (K) = **Adenolisianthus arboreus** (Spruce ex Prog.) Gilg in Engler & Prantl, Nat. Pflanzenfam. 4(2): 98. 1895.

Lisianthus auriculatus Benth. Pl. Hartweg. 226. 1846. TYPE: *Hartweg 1240* (K) = **Helia auriculata** (Benth.) O. Ktze. Rev. Gen. Pl. 2: 428. 1891.

Lisianthus Baltae (Weberb. & Gilg) Macbride, Fieldiana Bot. 13(5): 282. 1959 = **Symbolanthus Baltae** Weberb. & Gilg, Fedde, Repert. Sp. Nov. 2: 56. 1906. TYPE: *Weberbauer 4737* (B?).

Lisianthus bifidus HBK. Nov. Gen. & Sp. 3: 181. 1818. TYPE: "Crescit in montibus Novo-Granatensibus, prope fodinam Santanna," *Humboldt & Bonpland* (P) (Microfiche, IDC 6209. 72: III. 4!) = **Chelonanthus bifidus** (HBK.) Gilg in Engler & Prantl, Nat. Pflanzenfam. 4(2): 98. 1895.

Lisianthus breviflorus Benth. Hook. Jour. Bot. 2: 45. 1840. TYPE: Guiana, Sierra Mey, *Schomburgk* (K). According to Bentham (1876) and Nilsson (1970) this should be transferred to **Pagaea** Griseb.

Lisyanthus brevifolius (Cham.) Griseb. Gen. & Sp. Gent. 187. 1839 = **Helia brevifolia** Cham. Linnaea 8: 11. 1833. TYPE: "Lages [Brazil]," *Sellow.*

Lisianthus Brittonii Woodson, Fl. Trinidad & Tobago 2: 183. 1947. *Fide* Ewan, Contr. U.S. Nat. Herb. 29: 221. 1948 = *Chelonanthus arboreus* Britt. Bull. Dept. Agric. Trinidad & Tobago 19: 230. 1922.* TYPE: *Britton, Hazen & Mendelson 1295* (NY) = **Macrocarpaea arborea** (Britt.) Ewan, loc. cit.

Lisianthus browallioides Ewan, Proc. Biol. Soc. Wash. 64: 132. 1951. TYPE: *Allen 4932* (MO) = **Macrocarpaea browallioides** (Ewan) Robyns & Nilsson, Bull. Jard. Bot. Nat. Belg. 40: 13. 1970.

Lisyanthus caerulescens Aubl. Hist. Pl. Guiane 1: 207; 3: *t. 82.* 1775. TYPE: "Habitat in pratis humidis Guianae," *Aublet* (P) (Microfiche, IDC 6213. 23: IV. 4!) = **Irlbachia coerulescens** (Aubl.) Griseb. Gen. & Sp. Gent. 195. 1839.

Lisianthus calygonus Ruiz & Pav. Fl. Peruv. 2: 14. *t. 126.* 1799. TYPE: "In montibus frigidis Acomayo, Muña et Pallao, ad Chacahuassi et Achapatuman tractus," *Ruiz & Pavon* (MA) = **Symbolanthus calygonus** (Ruiz & Pav.) Gilg in Engler & Prantl, Nat. Pflanzenfam. 4(2): 99. 1895.

Lisianthus campanulaceus Desr. in Lam. Encycl. 3: 660. 1804. TYPE: "Guyane," *Richard* (P–JU) (Microfiche, IDC 6206. 512: III. 3!) = *Helia campanulacea* (Desr.) O. Ktze. Rev. Gen. Pl. 2: 428. 1891; referable to **Chelonanthus** (Griseb.) Gilg.

Lisianthus campanuloides Spruce ex Benth. Jour. Bot. Kew Misc. 6: 201. 1854. TYPE: "Right bank of Rio Negro, opposite Uananaca [Brazil]," *Spruce* (K) = **Chelonanthus campanuloides** (Spruce ex Benth.) Gilg in Engler & Prantl, Nat. Pflanzenfam. 4(2): 98. 1895.

Lisianthus cardonae (Gleason) Steyerm. Fieldiana Bot. 28: 498. 1953 = *Chelonanthus cardonae* Gleason, Brittonia 3: 189. 1939. TYPE: *Tate 1359* (NY). According to Nilsson (1970) this should be transferred to *Pagaea* Griseb.

*** Reference not seen.**

Lisianthus carinatus Desr. in Lam. Encycl. 3: 658. 1804 = **Tachiadenus carinatus** (Desr.) Griseb. Gen. & Sp. Gent. 201. 1839.

Lisianthus chelonoides L.f. Suppl. Pl. 134. 1781 (*nom. illegit.*, Art. 63) = *L. alatus* Aubl. = **Chelonanthus alatus** (Aubl.) Pulle.

Lisianthus chimantensis Steyerm. & Maguire, Mem. N.Y. Bot. Gard. 17(1): 461. 1967. TYPE: *Steyermark & Wurdack 374-A* (NY). According to Nilsson (1970) this does not fit into any existing genus.

Lisianthus corymbosus Ruiz & Pav. Fl. Peruv. 2: 14. *t. 124*. 1799. TYPE: "In Peruviae nemoribus inter Acomayo et Chinchao ad Pati praedium," *Ruiz & Pavon* (MA) = **Macrocarpaea corymbosa** (Ruiz & Pav.) Ewan, Contr. U.S. Natl. Herb. **29:** 242. 1948.

✓*Lisianthus crassicaulis* Mart. & Gal. Bull. Acad. Brux. **11**(1): 374. 1844. TYPE: *Galeotti 7176* (BR) = **Chelonanthus alatus** (Aubl.) Pulle *fide* Williams (1968).

Lisyanthus daturoides Griseb. Gen. & Sp. Gent. 177. 1839. TYPE: *Mathews 1317* (K) = **Symbolanthus daturoides** (Griseb.) Gilg in Engler & Prantl, Nat. Pflanzenfam. **4**(2): 99. 1895.

✓*Lisianthus densiflorus* Benth. Pl. Hartweg. 227. 1846. TYPE: *Hartweg 1241* (K) = **Macrocarpaea densiflora** (Benth.) Ewan, Contr. U.S. Natl. Herb. **29:** 232. 1948.

Lisianthus elegans Mart. Nov. Gen. & Sp. 2: 98. *t. 177*. 1827 = *L. pedunculatus* Cham. & Schlecht. = **Calolisianthus pedunculatus** (Cham. & Schlecht.) Gilg.

Lisianthus Elisabethae (Schomb.) Griseb. Linnaea **22:** 40. 1849 = *Leiothamnus Elisabethae* Schomb. Verh. Ver. Beförd. Gartenb. Königl. Preuss. Staaten **18:** 155. *t. 1*. 1847 = **Symbolanthus Elisabethae** (Schomb.) Gilg, Bot. Jahrb. **22:** 340. 1896.

Lisianthus fistulosus Poir. in Lam. Encycl. Suppl. 3: 514. 1816 = **Chelonanthus fistulosus** (Poir.) Gilg in Engler & Prantl, Nat. Pflanzenfam. **4**(2): 98. 1895.

Lisianthus frigidus Sw. Prodr. 40. 1788; Fl. Ind. Occ. 352. 1797. TYPE: "Incolit regionem muscosam montis la Soufriere Insulae Dominicae," *Ponthieu* (s!) = **Calolisianthus frigidus** (Sw.) Gilg in Engler & Prantl, Nat. Pflanzenfam. **4**(2): 101. 1895.

Lisianthus glaber L.f. Suppl. Pl. 134. 1781. TYPE: *Mutis*; specimen 213.2 (LINN) (Savage, 1945); (Microfiche, IDC 5057. 118. II. 2,3!) = **Macrocarpaea glabra** (L.f.) Gilg in Engler & Prantl, Nat. Pflanzenfam. **4**(2): 94. 1895.

Lisianthus glaucifolius Jacq. Coll. **1:** 64. 1787 = **Eustoma exaltatum** *fide* Grisebach (1845).

Lisianthus glaucifolius Nutt. Trans. Am. Phil. Soc. **5:** 197. 1837 = **Eustoma Russellianum** *fide* Grisebach (1845).

Lisyanthus gracilis Griseb. Gen. & Sp. Gent. 182. 1839. TYPE: St. Vincent, *Guilding* (K) = *L. uliginosus* Griseb. *fide* Index Kewensis = **Chelonanthus uliginosus** (Griseb.) Gilg.

Lisyanthus grandiflorus Aubl. Hist. Pl. Guiane **1:** 205; **3:** *t. 81.* 1775. TYPE: "Habitat in locis humidis Caienne & Guiane," *Aublet* (P) (Microfiche, IDC 6213. 23: IV. 5!) = **Chelonanthus grandiflorus** (Aubl.) Chod. & Hassl. Bull. Herb. Boiss. Ser. 2. **3:** 549. 1903.

Lisyanthus grandiflorus Willd. ex Griseb. Gen. & Sp. Gent. 182. 1839 (*nom. nud.*) = *L. uliginosus* Griseb. fide Grisebach (loc. cit.) = **Chelonanthus uliginosus** (Griseb.) Gilg.

Lisianthus imthurnianus Oliver, Trans. Linn. Soc. Ser. 2. **2:** 279. 1887. TYPE: *im Thurn 306* (K) = **Calolisianthus imthurnianus** (Oliver) Gleason, Bull. Torr. Bot. Club **56:** 402. 1929.

Lisianthus incarnatus Sessé & Moc. Fl. Mex. ed. 1. 39. 1893. *Ex char.* not referable to *Lisianthius.*

Lisianthus inflatus Mart. Nov. Gen. & Sp. **2:** 95. *t. 174.* 1827 = *L. speciosus* Cham. & Schlecht. *fide* Grisebach (1839) = **Calolisianthus speciosus** (Cham. & Schlecht.) Gilg.

Lisianthus Kunthii G. Don, Gen. Hist. **4:** 208. 1837 (*nom. illegit.*, Art. 63) = *L. angustifolius* HBK. = **Chelonanthus angustifolius** (HBK.) Gilg.

Lisyanthus leucanthus Lyall ex Griseb. Gen. & Sp. Gent. 202. 1839 (*nom. nud.*) = **Tachiadenus longiflorus** Griseb. loc. cit.

Lisyanthus longiflorus Boyer ex Griseb. Gen. & Sp. Gent. 202. 1839 (*nom. nud.*) = **Tachiadenus longiflorus** Griseb. loc. cit.

Lisianthus luteus Raf. Atl. Jour. 146. 1832 = **Eustoma Russellianum** *fide* Merrill (Index Rafinesquianum 192. 1949.)

Lisianthus macranthus Benth. Pl. Hartweg. 144. 1844. TYPE: *Hartweg 799* (K) = **Symbolanthus macranthus** (Benth.) Moldenke, Phytologia **2:** 235. 1947.

Lisianthus macrophyllus HBK. Nov. Gen. & Sp. **3:** 183. 1818. TYPE: "Crescit locis subfrigidus, in declivitate Parami de Almaguer, inter Pansitara et flumen," *Humboldt & Bonpland* (P) (Microfiche, IDC 6209. 72: III. 6!) = **Macrocarpaea macrophylla** (HBK.) Gilg in Engler & Prantl, Nat. Pflanzenfam. **4**(2): 94. 1895.

Lisianthus madagascariensis Spreng. Syst. **1:** 586. 1825 (*nom. illegit.*, Art. 63) = *L. trinervis* Desr. = **Tachiadenus trinervis** (Desr.) Griseb.

Lisyanthus Martii Griseb. Gen. & Sp. Gent. 187. 1839 (*nom. illegit.*, Art. 63) = *L. spathulatus* HBK. = **Helia spathulata** (HBK.) Gilg.

Lisyanthus Mathewsii Griseb. Gen. & Sp. Gent. 361. 1839. TYPE: *Mathews 1836* (K) = **Symbolanthus Mathewsii** (Griseb.) Gilg, Bot. Jahrb. **22:** 344. 1896.

Lisianthus nerioides Griseb. Linnaea **22:** 39. 1849. TYPE: *Moritz 1189* (B, but presumably destroyed) = **Symbolanthus nerioides** (Griseb.) Ewan, Proc. Biol. Soc. Wash. **63:** 165. 1950.

Lisyanthus oblongifolius (Mart.) Griseb. Gen. & Sp. Gent. 187. 1839 = **Helia oblongifolia** Mart. Nov. Gen. & Sp. **2:** 123. *t. 191.* 1827.

Lisyanthus obtusifolius Griseb. Gen. & Sp. Gent. 175. 1839. TYPE: Brazil, Sierra d'Estrella, *Sellow* (K) = **Macrocarpaea obtusifolia** (Griseb.) Gilg in Engler & Prantl, Nat. Pflanzenfam. **4**(2): 94. 1895.

✓*Lisianthus Oerstedtii* Griseb. Kjoeb. Vidensk. Meddel. **1853**: 54. 1854. TYPE: "Voxer mellem Matagalpa og Muimui; Provincem Segovia," *Oersted* = **Helia Oerstedtii** (Griseb.) O. Ktze. Rev. Gen. Pl. **2**: 428. 1891.

Lisianthus Ophiorriza Vell. Fl. Flum. **2**: 78. 1825 = **Metternichia principis** Mikan (Solanaceae) *fide* Sampiro & Peckolt, Arq. Mus. Nac. Rio de Janeiro **37**: 331–394. 1943.

Lisianthus ovalis Ruiz & Pav. Fl. Peruv. **2**: 13. 1799. TYPE: "In Peruviae nemoribus per Chinchao runcationes," *Ruiz & Pavon* (MA) = **Macrocarpaea ovalis** (Ruiz & Pav.) Ewan, Contr. U.S. Natl. Herb. **29**: 234. 1948.

Lisianthus ovatifolius Vell. Fl. Flum. **2**: 79. 1825 = *L. alpestris* Mart. *fide* Progel in Mart. Fl. Bras. **6**(1): 233. 1866.

Lisianthus paniculatus Spreng. Syst. Cur. Post. 340. 1827 = **Irlbachia elegans** Mart. *fide* Progel in Mart. Fl. Bras. **6**(1): 229. 1866.

Lisianthus parvifolius Desr. in Lam. Encycl. **3**: 660. 1804. TYPE: "Guyane," *Richard* (P–JU) (Microfiche, IDC 6206. 512: III. 4!) = **Irlbachia coerulescens** (Aubl.) Griseb. *fide* Grisebach (1839).

Lisianthus pauciflorus (Spruce ex Gilg) Macbride, Fieldiana Bot. **13**(5): 289. 1959 = **Symbolanthus pauciflorus** Spruce ex Gilg, Bot. Jahrb. 22: 340. 1896. TYPE: *Spruce 4429* (K).

Lisianthus pauciflorus Sessé & Moc. Pl. N. Hispan. ed. 1. 24. 1888. *Ex char.* not referable to *Lisianthius*.

Lisianthus pedunculatus Cham. & Schlecht. Linnaea **1**: 199. 1826. TYPE: "In Brasiliae interioribus regionibus," *Sellow* (HAL) = **Calolisianthus pedunculatus** (Cham. & Schlecht.) Gilg in Engler & Prantl, Nat. Pflanzenfam. **4**(2): 101. 1895.

Lisianthus pendulus Mart. Nov. Gen. & Sp. **2**: 94. *t. 172*. 1827 = **Calolisianthus pendulus** (Mart.) Gilg in Engler & Prantl, Nat. Pflanzenfam. **4**(2): 101. 1895.

Lisianthus pratensis HBK. Nov. Gen. & Sp. **3**: 180. 1818. TYPE: "Crescit locis gramineis prope Esmeraldem, in ripa Oronoci," *Humboldt & Bonpland* (P) (Microfiche, IDC 6209. 72: III. 2!) = *Helia pratensis* (HBK.) O. Ktze. Rev. Gen. Pl. **2**: 428. 1891; *ex char.* appears to be referable to **Chelonanthus** (Griseb.) Gilg.

Lisianthus princeps Lindl. Jour. Hort. Soc. **4**: 261. 1849. TYPE: *Schlim 419* (K) = **Lagenanthus princeps** (Lindl.) Gilg in Engler & Prantl, Nat. Pflanzenfam. **4**(2): 99. 1895.

Lisianthus pulcher Hook. Bot. Mag. **75**: *t. 4424*. 1849. TYPE: Colombia. Monte del Moro, *Purdie* (K) = **Purdieanthus pulcher** (Hook.) Gilg in Engler & Prantl, Nat. Pflanzenfam. **4**(2): 99. 1895.

✓*Lisianthus pulcherrimus* (Gilg) Donn. Sm. in Pittier, Prim. Fl. Costaric. **2**: 166. 1898 = **Symbolanthus pulcherrimus** Gilg, Bot. Jahrb. **22**: 314. 1896. TYPE: *Hoffmann 673*.

Lisianthus pulcherrimus Mart. Nov. Gen. & Sp. **2**: 97. *t. 176*. 1827 = **Calolisianthus pulcherrimus** (Mart.) Gilg in Engler & Prantl, Nat. Pflanzenfam. **4**(2): 101. 1895.

Lisianthus pumilus Benth. Jour. Bot. Kew Misc. **6:** 200. 1854. TYPE: Brazil, in inundated woods of the Rio Negro, near San Carlos, *Spruce* (K) = **Pagaea pumila** (Benth.) Gilg in Engler & Prantl, Nat. Pflanzenfam. **4**(2): 102. 1895.

Lisyanthus purpurascens Aubl. Hist. Pl. Guiane **1:** 201; **3:** *t. 79.* 1775. TYPE: "Habitat in fissuris humidis rupium montis Serpent," *Aublet* (P) (Microfiche, IDC 6213. 23: IV. 3!) = **Helia purpurascens** (Aubl.) O. Ktze. Rev. Gen. Pl. **2:** 428. 1891; referable to *Chelonanthus* (Griseb.) Gilg.

Lisianthus purpurascens HBK. Nov. Gen. & Sp. **3:** 182. 1818. TYPE: "Crescit locis inundatis, inter pagum San Fernando de Atabapo et cataractam Maypurensium," *Humboldt & Bonpland* (P) = *L. uliginosus* Griseb. *fide* Grisebach (1839) = **Chelonanthus uliginosus** (Griseb.) Gilg.

Lisianthus pyriformis (Gleason) Steyerm. Fieldiana Bot. **28:** 498. 1953 = **Chelonanthus pyriformis** Gleason, Bull. Torr. Bot. Club **58:** 450. 1931. TYPE: *Tate 747* (NY).

Lisianthus quelchii N.E. Brown, Trans. Linn. Soc. Ser. 2. Bot. **6:** 50. *t. 9, figures 6–9.* 1901. SYNTYPES: *McConnell & Quelch 106, 649* (K) = **Macrocarpaea quelchii** (N.E. Brown) Ewan, Contr. U.S. Natl. Herb. **29:** 233. 1948.

Lisyanthus racemosus Willd. ex Griseb. Gen. & Sp. Gent. 186. 1839 (*nom. nud.*) = *L. angustifolius* HBK. *fide* Grisebach (loc. cit.) = **Chelonanthus angustifolius** (HBK.) Gilg.

Lisianthus ramosissimus Benth. Jour. Bot. Kew Misc. **6:** 200. 1854. TYPE: *Schomburgk 989* (K) = **Pagaea ramosissima** (Benth.) Ewan, Proc. Biol. Soc. Wash. **63:** 165. 1950.

Lisianthus recurvus Benth. Jour. Bot. Kew Misc. **6:** 201. 1854. TYPE: Brazil, near Panuré, on the Río Uápes, *Spruce* (K) = **Pagaea recurva** (Benth.) Benth. & Hook. Gen. Pl. **2:** 814. 1876.

Lisianthus revolutus Ruiz & Pav. Fl. Peruv. **2:** 14. *t. 127.* 1799. TYPE: "In montibus altis frigidis Muna ad Saria," *Ruiz & Pavon* (MA) = **Macrocarpaea revoluta** (Ruiz & Pav.) Gilg in Engler & Prantl, Nat. Pflanzenfam. **4**(2): 94. 1895.

Lisianthus revolutus Poepp. ex Griseb. in DC. Prodr. **9:** 77. 1845 (*nom. nud.*) = *L. glaber* L.f. *fide* Grisebach (loc. cit.) = **Macrocarpaea glabra** (L.f.) Gilg.

Lisianthus roseus Sessé & Moc. Fl. Mex. ed. 1. 39. 1893. *Ex char.* this is not referable to *Lisianthius.*

Lisianthus Rusbyanus (Gilg) Macbride, Fieldiana Bot. **13**(5): 290. 1959 = **Symbolanthus Rusbyanus** Gilg, Bot. Jahrb. **22:** 344. 1896. TYPE: *Rusby 1227.*

Lisianthus Russellianus Hook. Bot. Mag. **65:** *t. 3626.* 1839 = **Eustoma grandiflorum** (Raf.) Shinners, Southwest. Nat. **2:** 41. 1957.

Lisianthus scabridulus Steyerm. Fieldiana Bot. **28:** 496. 1953. TYPE: *Steyermark 57979* (F!). According to Nilsson (1970) this should be transferred to **Pagaea** Griseb.

Lisianthus Schomburgkii Griseb. in DC. Prodr. **9:** 75. 1845. TYPE: *Schomburgk 298* (K) = **Chelonanthus Schomburgkii** (Griseb.) Gilg in Engler & Prantl, Nat. Pflanzenfam. **4**(2): 98. 1895.

Lisianthus sempervirens Mill. ex Steud. Nomencl. ed. 1. 486. 1821 (*nom. nud.*) = **Gelsemium sempervirens** (L.) Ait. (Loganiaceae).

Lisianthus spathulatus HBK. Nov. Gen. & Sp. 3: 181. 1818. TYPE: "Crescit locis calidissimis, humidis Insulae Pararumae, in flumine Oronoci," *Humboldt & Bonpland* (P) = **Helia spathulata** (HBK.) Gilg in Engler & Prantl, Nat. Pflanzenfam. 4(2): 101. 1895.

Lisianthus speciosus Cham. & Schlecht. Linnaea 1: 198. 1826. TYPE: "Crescit in Brasiliae regionibus interioribus," *Sellow* (HAL) = **Calolisianthus speciosus** (Cham. & Schlecht.) Gilg in Engler & Prantl, Nat. Pflanzenfam. 4(2): 101. 1895.

Lisianthus splendens Hook. Lond. Jour. Bot. 6: 264. 1847. TYPE: "Hills of red clay near Canoas, Province of Antioquia, New Grenada," *Purdie* (K) = **Lehmaniella splendens** (Hook.) Ewan, Caldasia 5: 87. 1948. Incorrectly attributed by Ewan (loc. cit.) to Gilg in Engler & Prantl, Nat. Pflanzenfam. 4(2): 101. 1895.

Lisianthus Spruceanus Benth. Jour. Bot. Kew Misc. 6: 202. 1854. TYPE: "Brazil, in grassy inundated places near San Gabriel, Río Negro," *Spruce* (K) = **Chelonanthus spruceanus** (Benth.) Pilger in Koch-Grünberg, Zwei Jahre unter den Indianern 2: 31. 1910.*

Lisianthus subcordatus Benth. Jour. Bot. Kew Misc. 6: 200. 1854. TYPE: "Brazil, near Panuré, on the Río Uápes," *Spruce* (K) = **Pagaea subcordata** (Benth.) Benth. & Hook. Gen. Pl. 2: 814. 1876.

Lisianthus Tatei (Gleason) Steyerm. Fieldiana Bot. 28: 498. 1953 = **Caloisianthus Tatei** Gleason, Bull. Torr. Bot. Club 58: 449. 1931. TYPE: *Tate 743* (NY). According to Nilsson (1970) this should be transferred to *Pagaea* Griseb.

Lisianthus tenuifolius Spreng. Syst. Cur. Post. 339. 1827. According to Nilsson (1970) this should be transferred to *Calolisianthus* (Griseb.) Gilg.

Lisianthus tetragono-alatus Steud. Nomencl. ed. 2. 2: 55. 1841 (*nom. nud.*) = *L. acutangulus* Mart. *fide* Progel in Mart. Fl. Bras. 6(1): 234. 1866 = **Calolisianthus acutangulus** (Mart.) Gilg.

Lisyanthus tetragonus Benth. Pl. Hartweg. 68. 1840. TYPE: *Hartweg 496* (K) = **Chelonanthus alatus** (Aubl.) Pulle *fide* Williams (1968).

Lisianthus thamnoides Griseb. Fl. Brit. W. Ind. Isl. 424. 1862. TYPE: Jamaica *Macfadyen* (K) = **Macrocarpaea thamnoides** (Griseb.) Gilg in Engler & Prantl, Nat. Pflanzenfam. 4(2): 94. 1895.

Lisianthus trifidus HBK. Nov. Gen. & Sp. 3: 182. 1818. TYPE: "Crescit inter Mariquitam et fodinam Santanna, Novo-Granatensium," *Humboldt & Bonpland* (P) (Microfiche, IDC 6209. 72: III. 5!); referable to *Chelonanthus* (Griseb.) Gilg.

Lisianthus trinervis Desr. in Lam. Encycl. 3: 659. 1804. TYPE: (P–JU) (Microfiche, IDC 6206. 512: III. 1!) = **Tachiadenus trinervis** (Desr.) Griseb. Gen. & Sp. Gent. 201. 1839.

Lisianthus trinervis Sessé & Moc. Fl. Mex. ed. 1. 39. 1893. *Ex char.* not referable to *Lisianthius.*

* Reference not seen.

Lisianthus tubiflorus Thou. ex Roem. & Schult. Syst. **4:** 788. 1819. TYPE: "In Madagascar," *Willdenow* (B) = **Tachiadenus tubiflorus** (Thou. ex Roem. & Schult.) Griseb. Gen. & Sp. Gent. 202. 1839.

Lisyanthus uliginosus Griseb. Gen. & Sp. Gent. 181. 1839 = **Chelonanthus uliginosus** (Griseb.) Gilg in Engler & Prantl, Nat. Pflanzenfam. **4**(*2*): 98. 1895.

Lisianthus vasculosus Griseb. Linnaea **22:** 37. 1849. SYNTYPES: *Karsten 27*, *Moritz 28* = **Symbolanthus vasculosus** (Griseb.) Gilg in Engler & Prantl, Nat. Pflanzenfam. **4**(*2*): 99. 1895.

Lisianthus virgatus Boj. ex Griseb. in DC. Prodr. **9:** 82. 1845 (*nom. nud.*) = **Tachiadenus gracilis** Griseb. loc. cit.

Lisianthus virgatus Prog. in Mart. Fl. Bras. **6**(1): 239. 1866. TYPE: In pascuis ad Ega prov. do Alto Amazonas Brazil," *Martius* (M) = **Adenolisianthus virgatus** (Prog.) Gilg in Engler & Prantl, Nat. Pflanzenfam. **4**(*2*): 98. 1895.

Lisianthus viridiflorus Mart. Nov. Gen. & Sp. **2:** 94. *t. 173.* 1827 = **Chelonanthus viridiflorus** (Mart.) Gilg in Engler & Prantl, Nat. Pflanzenfam. **4**(*2*): 98. 1895.

Lisianthus viscosus Ruiz & Pav. Fl. Peruv. **2:** 14. *t. 125.* 1799. TYPE: "In altis locis Muña ad Tambo," *Ruiz & Pavon* (MA) = **Macrocarpaea viscosa** (Ruiz & Pav.) Gilg in Engler & Prantl, Nat. Pflanzenfam. **4**(*2*): 94. 1895.

Lisianthus volubilis Salisb. Prodr. 137. 1796 = **Gelsemium sempervirens** (L.) Ait. (Loganiaceae).

Lisianthus zeylanicus Spreng. Syst. **1:** 586. 1825 = **Exacum zeylanicum** *fide* Grisebach (1845).

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SEEDS FROM SURFACE SOILS IN A TROPICAL REGION OF VERACRUZ, MEXICO *

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IN THE DEVELOPMENT of studies on the secondary vegetation of lowland tropical regions of Mexico (Gómez-Pompa, 1971; Gómez-Pompa et al., 1964; Sarukhán, 1964; Sousa, 1964) it has been very clear that additional studies must be carried on if we want to learn more about the process of secondary succession. An important factor in the initiation of a secondary succession is the amount of seeds stored in the soil ("seed crop" or "floristic potential"). This area of ecological research has been developed to some extent in temperate regions (Champness, 1949; Champness & Morris, 1948; Milton, 1936, 1939, 1943, and 1948; Brenchley, 1918; Brenchley & Adam, 1915; Ovington, 1955; Olmsted & Curtis, 1946), but no records exist for tropical areas.

The importance of seeds in the soil for the development of secondary succession in the tropical regions may be even greater than in temperate ones, because the first colonizers will open the way for the other species (including the primary species) and this process of colonization and growth is very rapid in the humid tropics (Sarukhán, 1964; Budowski, 1965; Rico, 1972). Several hypotheses have been proposed to explain different aspects of succession but it is clear that what is needed is experimental work to obtain data as a basis for some of these hypotheses (Gómez-Pompa, 1967).

The opportunity for initiating such studies arose with the establishment, by the National University of Mexico, of the Tropical Biological Station at Los Tuxtlas, Veracruz, in an evergreen rain forest region.

The main objectives of the work reported in this paper were: to find a method for doing such investigation in a tropical region; to evaluate the difference between the seeds of a secondary vegetation soil and a primary one; to discover some of the relationships to various environmental factors in the two conditions, especially temperature and floristic composition of the surrounding vegetation. We were also looking for some clues to solve the problem of the trigger mechanisms in the germination of seeds of recently opened soils, which have a whole set of species different from the

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primary vegetation type (Oosting & Humphreys, 1940, 1947; Vázquez & Gómez-Pompa, 1971).

MATERIALS AND METHODS

Four areas were chosen for sampling purposes, two in secondary vegetation and two in primary vegetation. In each area a quadrat of 100 m^2 was selected for floristic, environmental, and soil studies. In each of the quadrats sixteen samples of soil were taken at random for seed germination purposes. In order to understand the changes through time these were repeated eight times during the year of the study. So, a total of eight time periods were surveyed. In each quadrat a floristic inventory was compiled to obtain an idea of the species growing in that soil site. Air (75 cm.) and soil (2 cm. deep, FIGURE 1) temperature and records of relative humidity

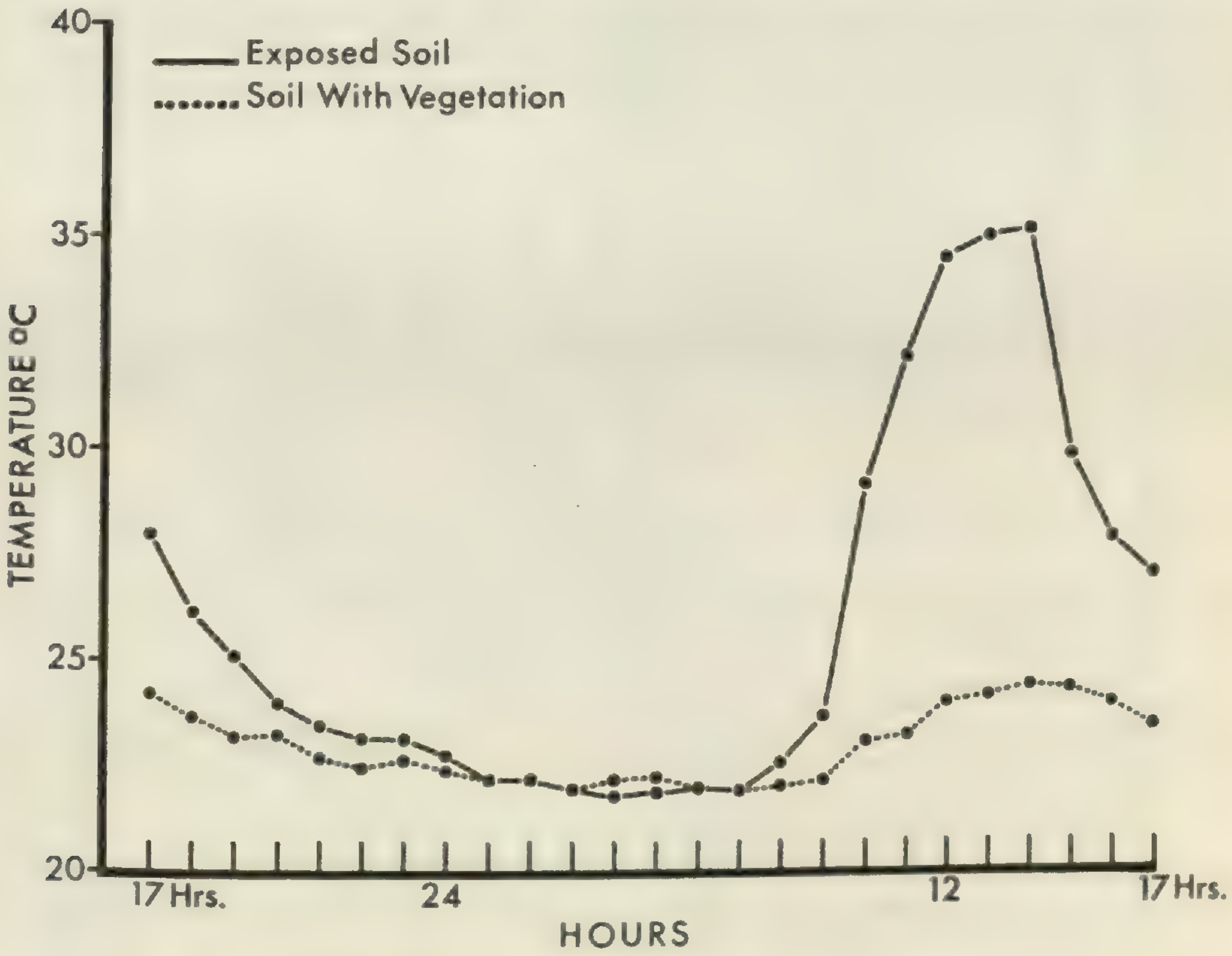


FIGURE 1. Soil temperature (24 hrs.).

were taken through the year in all the sampling sites, and precipitation data were available from the meteorological station in the Biological Station located a few hundred meters from the farthest point of the sampling sites (FIGURE 2).

The soil samples were taken with a specially constructed cylindrical metal sampler 477 cm^3 in volume. Each soil sample was placed in a plastic bag and taken to a "germination house." There each sample was put on 400 gms. of vermiculite and placed in plastic plates in the "house."

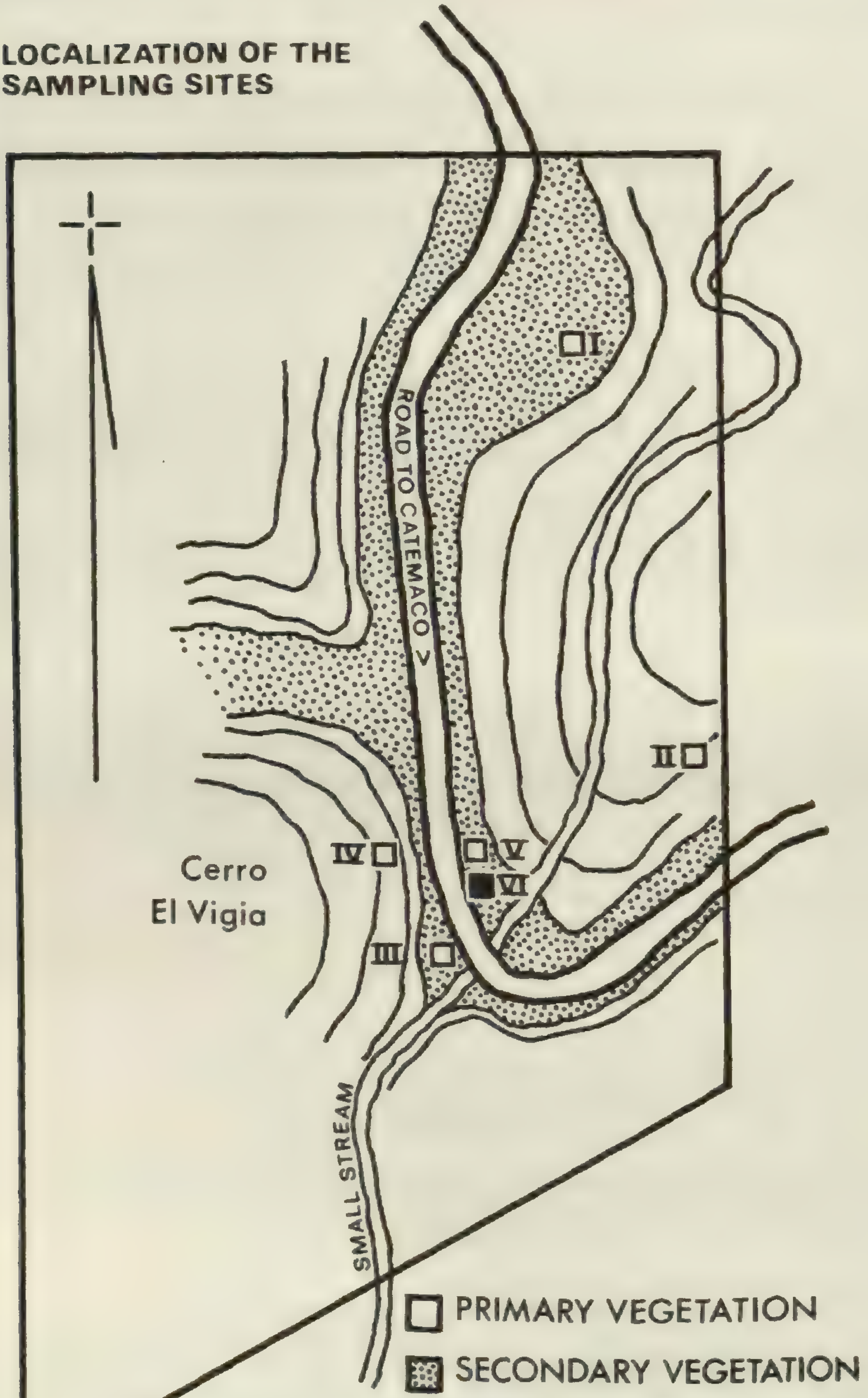


FIGURE 2. Localization of the sampling sites.

Germination was selected for evaluating the soil seed crop instead of a direct observation and count of the seeds in the soil (Barbour & Lange, 1967). The reasons for this are various but the most important one is the difficulty of identification of species by seeds (especially difficult for tropical species).

The only objective of the "germination house" was to protect the soil samples from seed contamination. It had a ceiling of thin plastic and walls of mosquito netting to permit free circulation of air. Temperature and humidity data were taken in this house also. The plates were circulated during the six weeks they remained in the house in order to have homogeneous conditions. They were watered daily with equal amounts of water (3.5 liters).

Four plates with only vermiculite were always in the house as controls for possible contamination. None were contaminated during the study.

After six weeks the plates were analyzed for the germinated plants. A count was made of the number of different species and number of individuals of each species. The species that we were not able to identify botanically were transplanted to a "nursery" for continued growth (age) and future identification. As the flora of the Station is known quite well (Gómez-Pompa & Nevling, 1971) the identification is not as unattainable a task as it may appear. Voucher specimens of the seedlings and of the "aged" plants were prepared and deposited in the National Herbarium of Mexico (MEXU). We want to acknowledge the help of Dr. L. I. Nevling, Jr., with the identification of some of the difficult species and that of Dr. R. McVaugh who identified some of the Compositae.

RESULTS

Description of the region of Los Tuxtlas. The Tropical Biological Station is located in the Sierra de los Tuxtlas in the southern part of the state of Veracruz in the parallel 18° 30′ N and in the meridian 95° W.

Because of its orography the region is one of the most humid areas in

FIGURE 3. **Meteorological records from Coyame Station and the Estacion de Biología Tropical Los Tuxtlas** [3]

METEOROLOGICAL STATION	MEAN TEMP. (° C)	EXTREME MAX. TEMP. (° C)	EXTREME MIN. TEMP. (° C)	RELATIVE HUMIDITY %	RAINFALL (mm.)
COYAME [1]	23.6	38.5 (May)	9.5 (January)	—	4419.8
ESTACIÓN DE BIOL. TROP. LOS TUXTLAS [2]	25.0	43.3 (June)	12.2 (February)	81.9	4012.0

[1] The record covers the period from 1921 to 1970.
[2] The record covers one year (1970).
[3] Taken from Soto (1972).

FIGURE 4. **Soil properties** *

DEPTH (cm.)	COLOR	TEXTURE	pH	% ORGANIC MATTER	NITRIC NITROGEN KG./HA	CALCIUM KG./HA	PHOSPHORUS KG./HA	POTASSIUM KG./HA
0–30	reddish brown	clay loam	6.25	4.45	27	3129	14.6	413
30–60	reddish brown	clay loam	6.20	1.37	14	1498	7.2	90
60–100	reddish brown	clay loam	5.80	1.71	14	1735	7.9	124

* Flores, 1971.

the Gulf Coast of Mexico and precipitation of more than 4 meters per year has been recorded (García, 1971) from nearby stations. Data available from the meteorological records of the station during the year of the study are recorded in FIGURE 3, but cannot be used for evaluation of climate because of lack of comparative data from preceding years. The closest station which can give a better idea of the climate is Coyame (FIGURE 3).

The vegetation of the region is composed of many types produced by variations in temperature, precipitation, and soil properties (Gómez-Pompa, 1972; Sousa, 1968), with a very rich floristic composition. Floristic differences may be seen within short distances. In adjacent areas floristic variations arise chiefly from secondary successional stages (Gómez-Pompa, 1971).

Description of the Station. The station is located on the NE slope of the Sierra of San Martín, very close to the coast, and is covered mainly by a High Evergreen Selva of an average of 30 meters in height, and a few secondary vegetation sites along the main road crossing the station property (FIGURE 2) on one side. The sampling was done on the lower slopes of a small hill (Cerro El Vigía) belonging to the station (as can be seen in FIGURE 2).

The soil in the station is a brown and yellow acid soil derived from volcanic ash. Some of its characteristics are indicated in FIGURE 4.

Description of the sampled sites. SITE 1. This area is covered with secondary vegetation about five years old. Before that time it was cultivated with corn for about one or two years, and before the corn, it was a primary High Evergreen Selva. This quadrat is located on a slope of about 15 to 30° inclination. There is a considerable quantity of volcanic alluvial rock over the surface (40%). The average height of the upper stratum is about 7 to 8 meters. The altitude is 108 meters above sea level. Some records of soil and air temperature during the study are shown in FIGURE 5, those of the humidity and dew point in FIGURE 6. The species collected are listed in FIGURE 7.

SITE 2. This area is covered with a High Evergreen Selva about 30 meters tall. The quadrat is located on a slope of about 15 to 30° inclination. It is also covered with a considerable proportion of volcanic rocks (30%). The altitude is 120 meters above sea level. Soil and air temperature are shown in FIGURE 5, records of humidity in FIGURE 6. The species collected are listed in FIGURE 7.

SITE 3. When the study started, the area was covered by secondary vegetation of two months' duration. The area was covered before that by secondary vegetation for a few months and earlier it was a Tall Evergreen Selva. The quadrat is located on a slope of about 20 to 40° inclination. Free of rocks. Observations of soil and air temperature and humidity are shown in FIGURES 5 and 6. The species collected are listed in FIGURE 7.

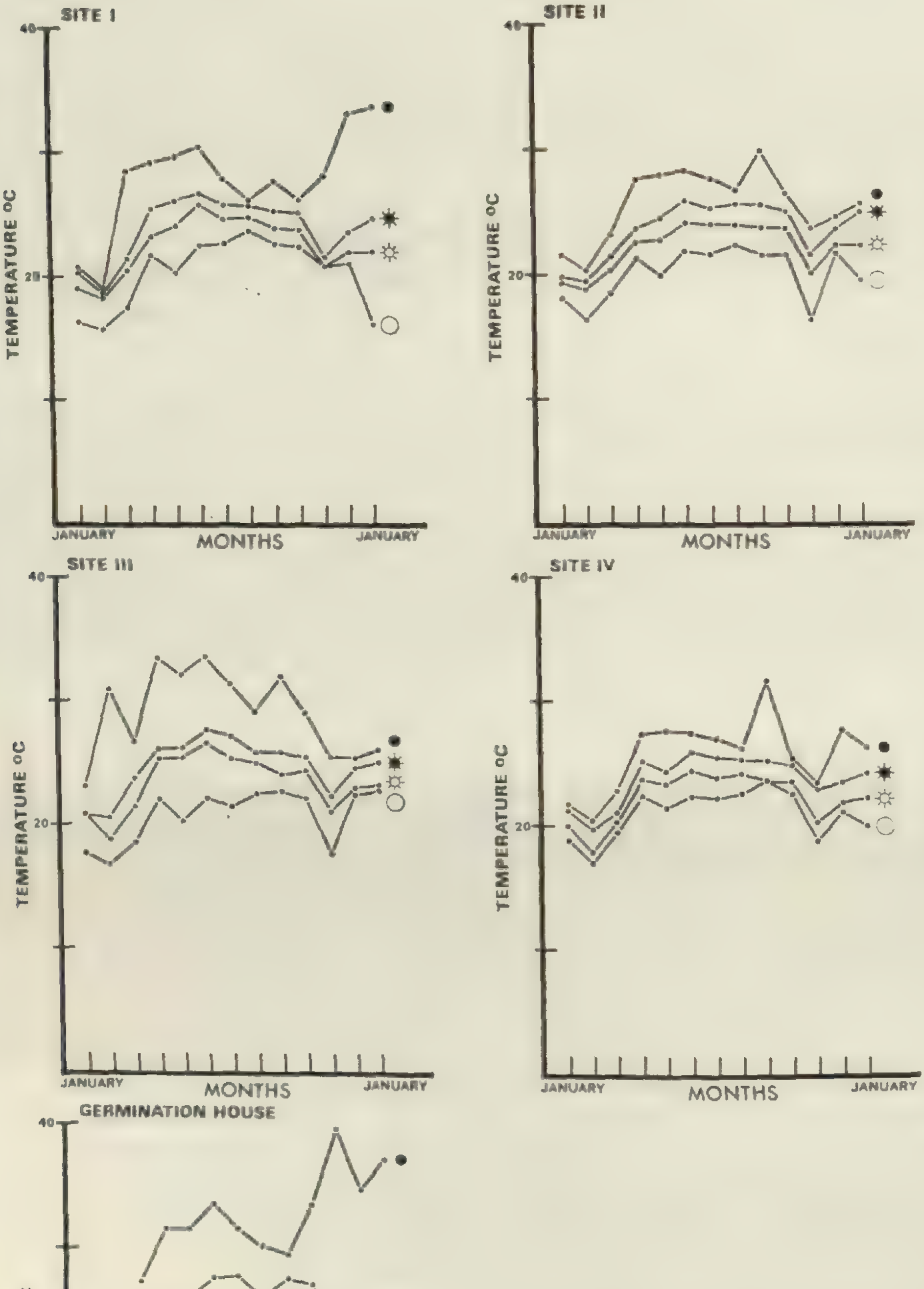


FIGURE 5. Air and Soil Temperature: ● max. temperature of air; ○ min. temperature of air; ✻ soil temperature after insolation (4:30 P.M.); ☼ soil temperature before insolation (7:30 A.M.).

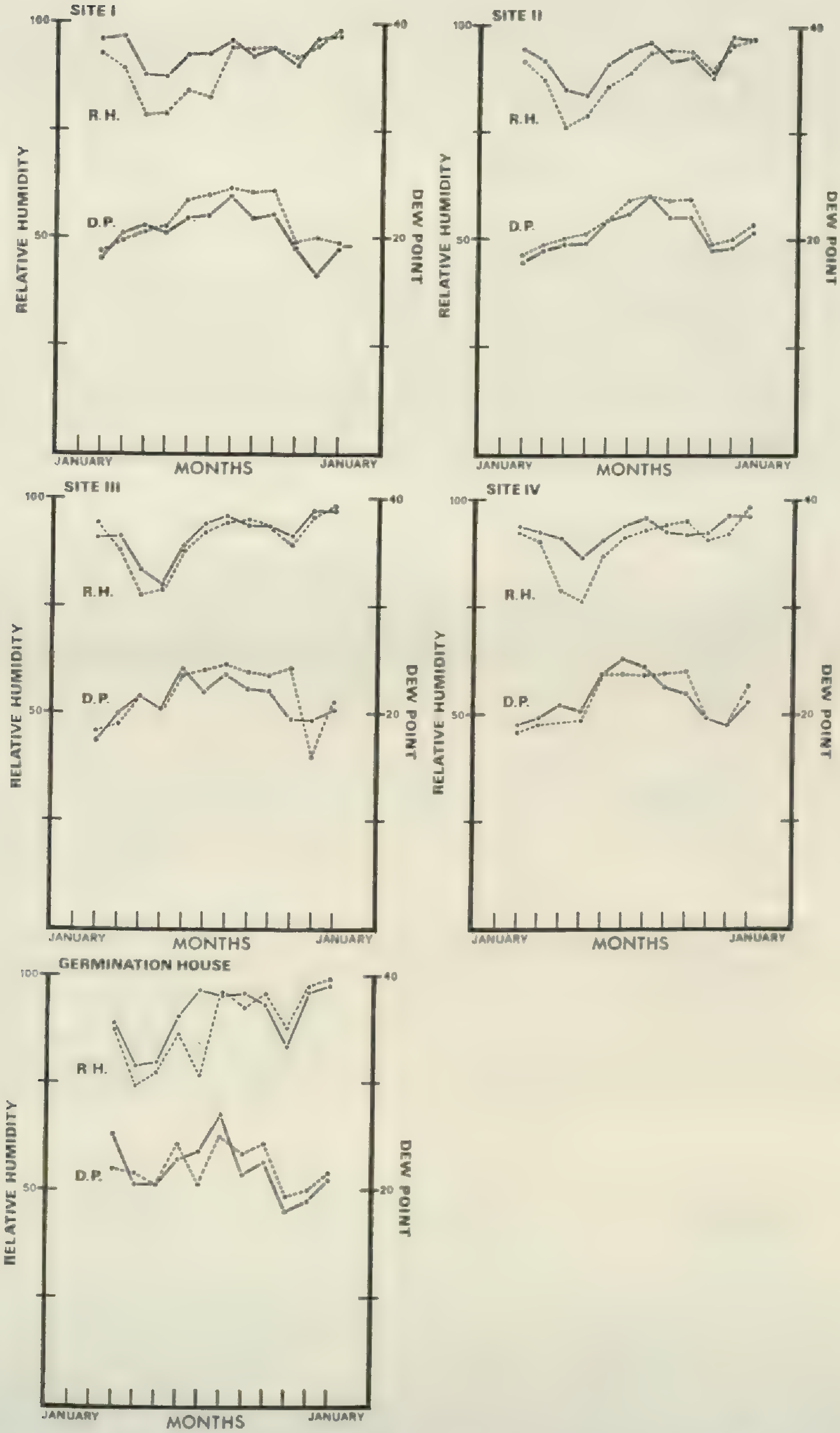


FIGURE 6. Air humidity: ——— 7:30 A.M.; . . . . . 4:30 P.M.

FIGURE 7. **Flora of the sampling sites**

SPECIES	SITE I	SITE II	SITE III	SITE IV
Aneilema geniculata	+			
Anthurium myosuroides	+	+		
Astrocaryum mexicanum	+	+		+
Cardiospermum halicacabum		+	+	+
Casearia arguta		+		
Cecropia obtusifolia	X	+	+	
Celtis iguanaea		+		
Citharexylum pterocladum		+	+	
Cupania macrophylla		+	+	
Cymbopetalum baillonii		+	+	
Dieffenbachia seguine		+	+	
Eupatorium sp.		+		
Hamelia axillaris		+		
Litachne pauciflora		+		
Myriocarpa longipes		+	+	
Passiflora sp.		+		
Piper auritum		+	+	
Piper hispidum		+	+	
Piper lapathifolium		+		
Piper martensianum		+		
Piper aff. *sanctum*		+		
Renealmia aromatica		+		
Robinsonella mirandae	X	+	+	
Solanum sp.		+		
Syngonium podophyllum		+	+	+
Aegiphila costaricensis		+		
Aphelandra aurantiaca		+	+	
Costus spicatus	X	+	+	+
Chamaedorea sp.		+		+
Chamaedorea tepejilote		+		
Dendropanax arboreus		+		
Diplazium sp.		+	+	+
Guarea bijuga		+		
Hiraea obovata		+		+
Ilex condensata		+		
Justicia sp.		+	+	
Lomariopsis sp.		+		
Lucuma durlandii		+		
Malmea depressa		+		
Monstera tuberculata		+		
Nectandra salicifolia		+		
Philodendron sanguineum		+		+
Pleuranthodendron mexicana	X	+		
Polypodium sp.		+		
Pseudolmedia oxyphyllaria		+		+
Reinhardtia gracilis		+		+

FIGURE 7 *Continued*

SPECIES	SITE I	SITE II	SITE III	SITE IV
Serjania sp.		+		
Syngonium donnell-smithii		+		
Tradescantia sp.		+		
Trichilia japurensis		+		
Acalypha deppeana			+	
Acalypha schiedeana	X		+	
Ageratum conyzoides	X		+	
Aspidosperma megalocarpon			+	
Brosimum alicastrum	X		+	
Calathea microcephala			+	
Campelia zanonia			+	
Cestrum sp.			+	
Cirsium mexicanum	X		+	
Clematis dioica			+	
Clibadium arboreum	X		+	
Elvira biflora			+	
Enterolobium cyclocarpum	X		+	
Eupatorium sp.			+	
Eupatorium macrophyllum	X		+	
Ficus sp.			+	+
Heliocarpus appendiculatus	X		+	
Inga spuria			+	+
Iresine celosia	X		+	
Jacobinia sp.	X		+	
Lygodium sp.			+	
Ocotea dendrodaphne			+	
Omphalea cardiophylla			+	
Paullinia pinnata			+	
Piper sp.			+	
Pothomorphe umbellata	X		+	
Rapanea myricoides			+	
Sapium lateriflorum			+	
Sicyos deppei			+	
Solanum amazonium			+	
Solanum nigrum	X		+	
Spigelia anthelmia			+	
Spondias mombin			+	
Taraxacum officinale			+	
Verbesina greenmani	X		+	
Vernonia deppeana	X		+	
Anthurium sp.				+
Croton macrodontus				+
Chamaedorea aff. *lindeniana*				+
Dieffenbachia oerstedii				+
Eugenia trikii				+
Oreopanax capitatum				+
Paullinia costaricensis				+

FIGURE 7 *Continued*

SPECIES	SITE I	SITE II	SITE III	SITE IV
Poulsenia armata				+
Salacia megistophylla				+
Thelypteris ghiesbreghtii				+
Trophis mexicana				+
Trophis racemosa				+

SYMBOLS: X Species of which seeds were found in the soil samples.
+ Specimens of each species were deposited at the Herbario Nacional, UNAM (MEXU).

SITE 4. This area is located in a High Evergreen Selva similar to SITE 2, but with a lower inclination of only 8 to 10°; it is almost free of rocks at an altitude of 131 meters above sea level. Records of soil and air temperature and humidity are tabulated in FIGURES 5 and 6. The species collected are listed in FIGURE 7.

Site of the germination house. The experiments were carried on in an area that simulated an open soil free of plants and not covered by shade from any plant. The area was near the laboratories of the station in order to be maintained and looked after properly. A few soil samples were brought to Mexico City to be germinated in the greenhouses of the Botanic Garden for comparison and indication of possible differences, but since in all cases there were none, we proceeded with only the analysis of data from our local germination house. Readings of air and soil temperature and humidity in the house are recorded in FIGURES 5 and 6.

Germination of the seeds. Germination was abundant and started almost immediately (after a few days). There were a few seedlings observed that did not continue normal growth; in some cases these were transplanted and care was taken to look for microenvironments. In some cases we were fortunate that these plants continued to grow, in other cases, however, they died. This problem will be discussed later as a possibility for future studies.

More than 80 percent of the species are now identified, (FIGURE 8), leaving only a few still to be determined.

The following species were identified in living condition in the soils of the sampling sites:

QUADRAT 1

Phytolacca decandra L.
Bidens pilosa L.
Iresine celosia L.
Euphorbia heterophylla L.
Neurolaena lobata (L.) R. Br.
Eupatorium sp.

Ageratum conyzoides L.
Clibadium arboreum Donn. Sm.
Clibadium grandifolium Blake
Paspalum sp.
Dioscorea sp.
Solanum torvum Sw.
Verbesina greenmani Urb.
Urera caracasana (Jacq.) Griseb.
Amaranthus hybridus L.
Spigelia palmeri Rose
Heliocarpus aff. *donnell-smithii* Rose
Emilia sonchifolia (L.) DC.
Schistocarpha oppositifolia (Kuntze) Rydb.

QUADRAT 2

Solanum cervantesii Lag.
Lasiacis papillosa Swallen
Phytolacca decandra L.
Cecropia obtusifolia Bert.
Heliocarpus aff. *donnell-smithii* Rose
Bignoniaceae (unidentified)
Turpinia occidentalis (Sw.) G. Don
Sapium lateriflorum Hemsl.
Iresine celosia L.
Belotia campbellii Sprague
Erechtites hieracifolia (L.) Raf.
Pothomorphe umbellata (L.) Miq.
Eupatorium macrophyllum L.
Neurolaena lobata (L.) R. Br.
Ageratum conyzoides L.
Clibadium arboreum Donn. Sm.
Paspalum sp.
Sida acuta Burm.
Trema micrantha (L.) Blume
Robinsonella mirandae Gómez-Pompa
Panicum trichoides Sw.
Bidens pilosa L.
Enterolobium cyclocarpum (Jacq.) Griseb.
Axonopus compressus (Sw.) Beauv.
Amaranthus hybridus L.
Pleuranthodendron mexicana (Gray) L. Wms.

QUADRAT 3

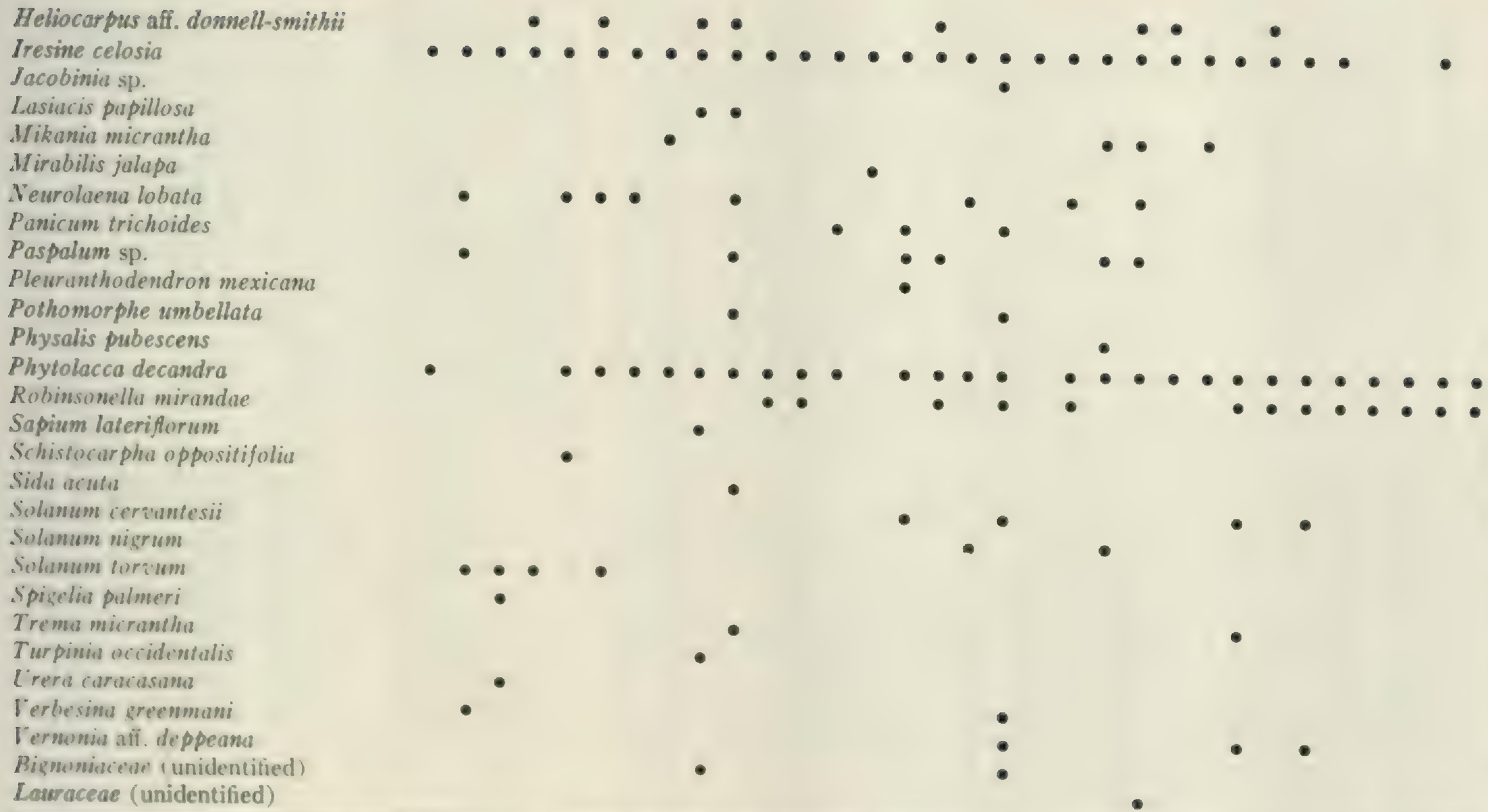
Solanum nigrum L.
Phytolacca decandra L.
Neurolaena lobata (L.) R. Br.
Heliocarpus appendiculatus Turcz.
Bidens pilosa L.
Iresine celosia L.
Pothomorphe umbellata (L.) Miq.
Eupatorium macrophyllum L.
Eupatorium aff. *pansamalense* Rob.
Bignoniaceae (unidentified)
Panicum trichoides Sw.
Vernonia aff. *deppeana* Less.
Solanum cervantesii Lag.
Robinsonella mirandae Gómez-Pompa
Verbesina greenmani Urb.
Eupatorium sp.
Ageratum conyzoides L.
Physalis pubescens L.
Paspalum sp.
Mikania micrantha HBK.
Brosimum alicastrum Sw.
Heliocarpus donnell-smithii Rose
Lauraceae (unidentified)

QUADRAT 4

Phytolacca decandra L.
Croton draco Schlecht.
Vernonia aff. *deppeana* Less.
Iresine celosia L.
Solanum cervantesii Lag.
Robinsonella mirandae Gómez-Pompa
Trema micrantha (L.) Blume
Cecropia obtusifolia Bert.
Heliocarpus donnell-smithii Rose
Eupatorium sp.
Costus spicatus (Jacq.) Sw.
Ageratum conyzoides L.
Desmodium adscendens (Sw.) DC.

FIGURE 8. **Species found in the soil samples**

SPECIES *	SITE I								SITE II								SITE III								SITE IV							
	Mar 19	May 3	Jun 28	Aug 10	Sep 27	Nov 15	Jan 4	Feb 18	Mar 19	May 3	Jun 28	Aug 10	Sep 27	Nov 15	Jan 4	Feb 18	Mar 19	May 3	Jun 28	Aug 10	Sep 27	Nov 15	Jan 4	Feb 18	Mar 19	May 3	Jun 28	Aug 10	Sep 27	Nov 15	Jan 4	Feb 18
Acalypha schiedeana																			•		•											
Ageratum conyzoides		•		•	•		•			•		•			•					•								•			•	
Amaranthus hybridus			•				•							•	•								•									
Axonopus compressus													•																			
Belotia campbellii									•	•																						
Bidens pilosa	•	•											•				•				•											
Brosimum alicastrum																						•	•	•								
Cecropia obtusifolia									•	•																•						
Cirsium mexicanum			•																		•											
Clibadium arboreum		•	•	•		•		•																								
Clibadium grandifolium		•																														
Costus spicatus																													•			
Croton draco																																
Desmodium adscendens																															•	
Dioscorea sp.		•																														
Emilia sonchifolia				•																												
Enterolobium cyclocarpum													•																•			
Erechtites hieracifolia														•																		
Eupatorium sp.		•	•		•	•	•								•	•				•	•	•	•	•					•		•	
Eupatorium macrophyllum														•					•			•										
Eupatorium pansamalense																			•													
Eupatorium pycnocephalum													•																			
Euphorbia heterophylla		•																														
Heliocarpus appendiculatus																				•												



* Specimens of each species were deposited at the Herbario Nacional, UNAM (MEXU).

DISCUSSION

From the results we have up to now, we can distinguish several groups of species in relation to their presence in the soils sampled:

Species present in the soil all year in most samples:

Phytolacca decandra L.
Eupatorium sp.
Neurolaena lobata (L.) R. Br.
Ageratum conyzoides L.
Iresine celosia L.
Robinsonella mirandae Gómez-Pompa

Species present for only a short period of time:

Brosimum alicastrum Sw.
Cecropia obtusifolia Bert.
Vernonia aff. *deppeana* Less.
Mikania micrantha HBK.
Belotia campbellii Sprague

Species present all year but in few samples:

Clibadium arboreum Donn. Sm.
Bidens pilosa L.
Amaranthus hybridus L.
Heliocarpus donnell-smithii Rose
Paspalum sp.
Solanum torvum Sw.

Secondary species present in soil of the primary rain forest:

Erechtites hieracifolia (L.) Raf.
Cecropia obtusifolia Bert.
Croton draco Schlecht.
Desmodium adscendens (Sw.) DC.
Costus spicatus (Jacq.) Sw.
Sida acuta Burm.
Belotia campbellii Sprague
Trema micrantha (L.) Blume
Pleuranthodendron mexicana (Gray) L. Wms.
Axonopus compressus (Sw.) Beauv.
Mirabilis jalapa L.
Eupatorium pycnocephalum Less.

Primary species present in soil of the secondary vegetation:

Brosimum alicastrum Sw.
Lauraceae (unidentified)

Secondary species found exclusively in the secondary vegetation:

Lasiacis papillosa Swallen
Solanum nigrum L.
Euphorbia heterophylla L.
Eupatorium aff. *pansamalense* Rob.
Physalis pubescens L.
Emilia sonchifolia (L.) DC.
Paspalum sp.
Schistocarpha oppositifolia (Kuntze) Rydb.
Heliocarpus appendiculatus Turcz.
Clibadium grandifolium Blake
Dioscorea sp.
Solanum torvum Sw.
Urera caracasana (Jacq.) Griseb.
Verbesina greenmani Urb.
Spigelia palmeri Rose
Cirsium mexicanum DC.
Acalypha schiedeana Schlecht.
Jacobinia sp.
Mikania micrantha HBK.

Primary species found exclusively in the primary vegetation:

Turpinia occidentalis (Sw.) G. Don
Enterolobium cyclocarpum (Jacq.) Griseb.
Sapium lateriflorum Hemsl.

It is obvious from all the preceding lists that by far the most important floristic element in the soil is composed of secondary species, which are

also the species having longer periods of dormancy (Pijl, 1969). This means that a primary forest can not be restored if all the trees from adjacent areas are destroyed. This is another extremely important argument for conserving large and numerous pieces of tropical selvas.

It is also evident that floristic potential in the soil is a very important element in the direction of the succession. The time of year is also important from this point of view because different species are available in the soil at different seasons.

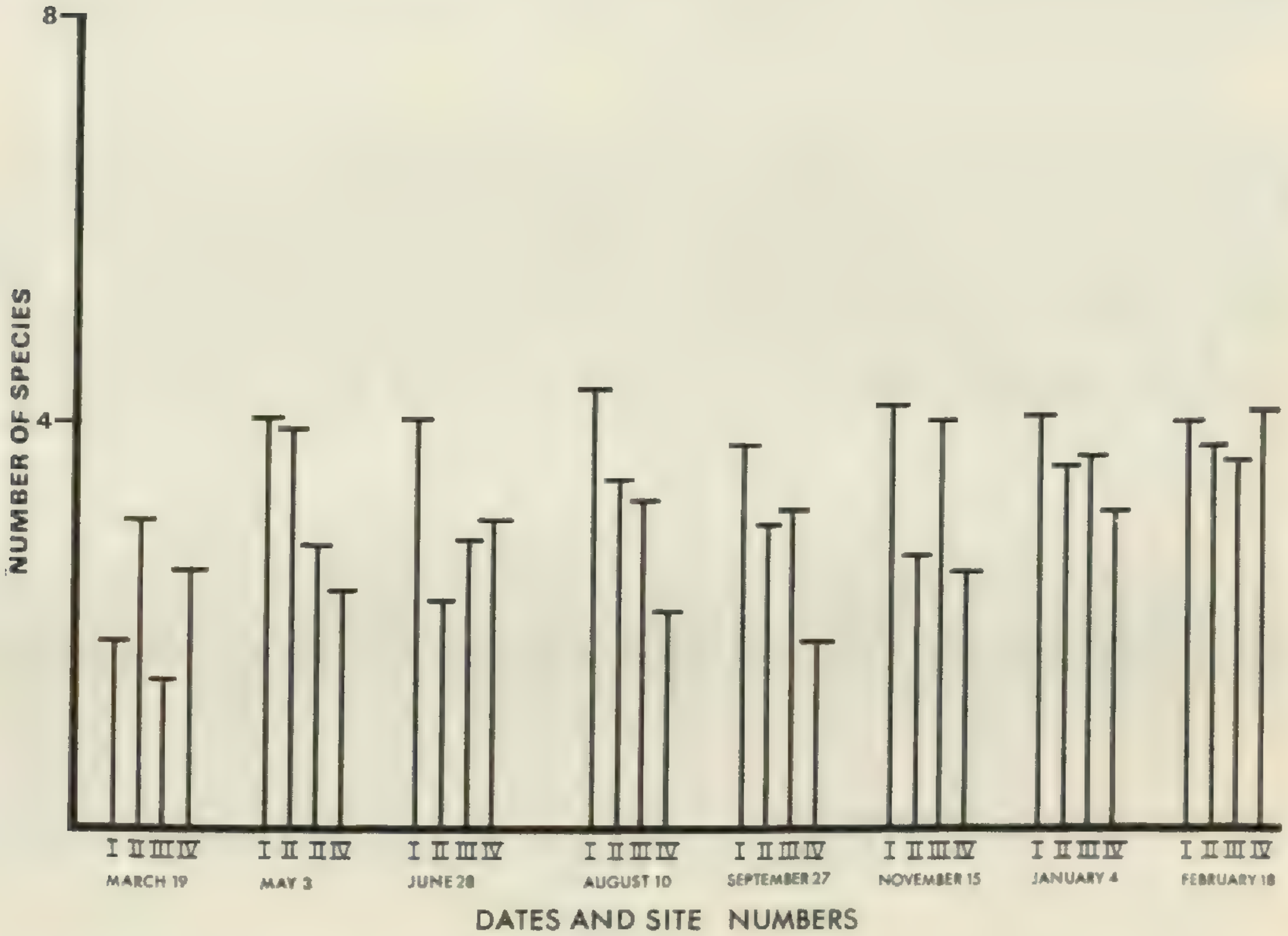


FIGURE 9. Mean of the number of species.

It is a striking fact that in the soils of the primary selvas there is a floristic potential of secondary species ready to function after clearance of the forest. The factor keeping the secondary seeds dormant is unknown and worth investigating, because the species represented are not found in the primary forest. Also the trigger mechanisms should be studied in order to clarify the factors involved in the succession.

We are well aware that in this work we have only scratched the surface of the problem and that there are many other ways to trigger the germination of soil seeds which under the method used (temperature variation, humidity, light, chemicals, etc.) have not germinated or germinated but did not continue growing, probably because the right combination of conditions was not attained. We hope in the future to obtain new data to increase our understanding of this problem.

One of the most interesting fields yet to be explored is that of seed and fruit dispersal (Smythe, 1970) because it is perfectly clear that the

floristic potential can not be built if the seed has not arrived at a given location.

It is also important to add that there is a great need for floristic studies with a solid ecological approach that can be used to interpret the behavior of different species under different ecological conditions and also to study their evolution in connection with secondary environments (Gómez-Pompa, 1971).

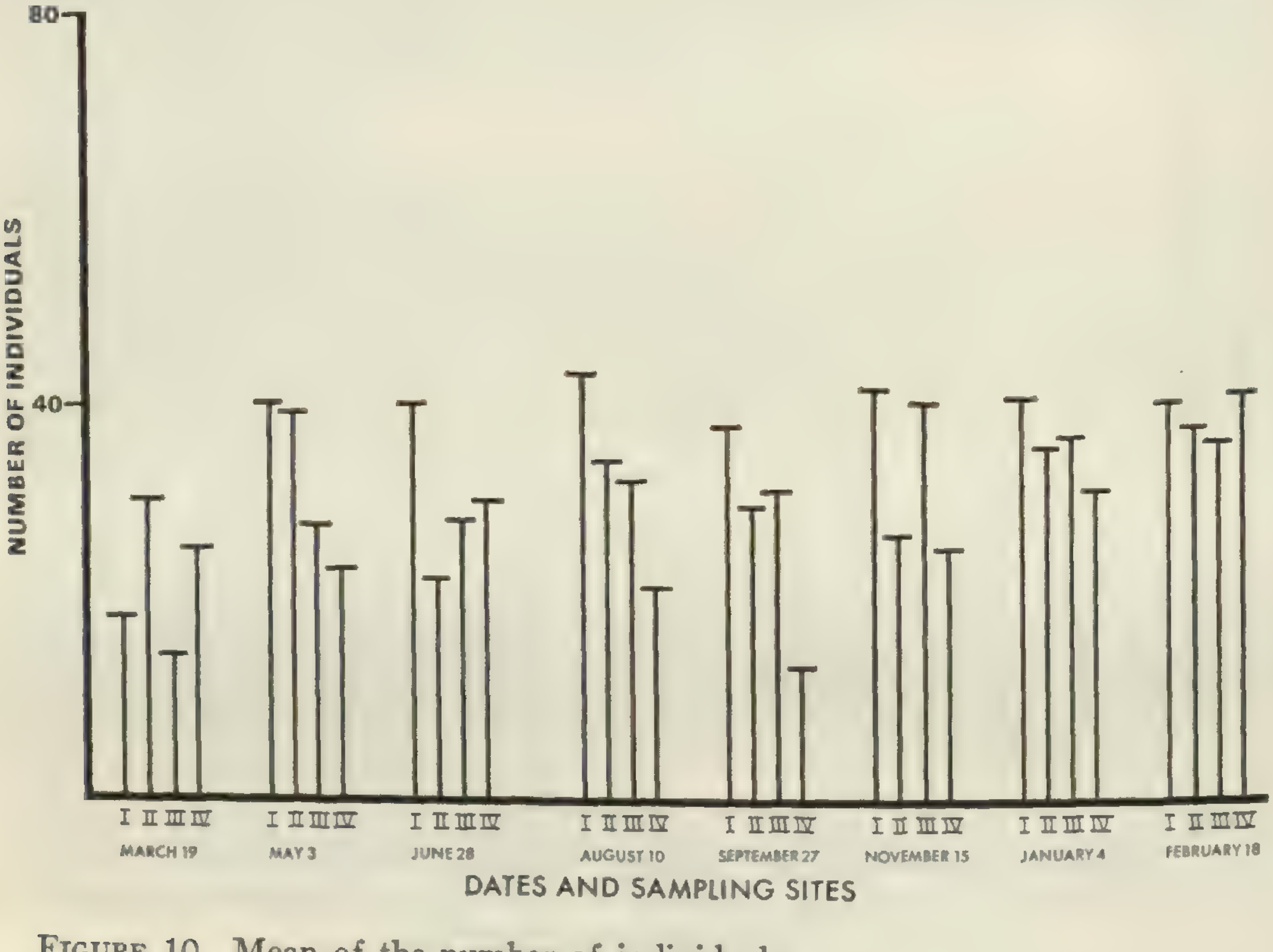


FIGURE 10. Mean of the number of individuals.

The data on the number of species and of individuals per sampling are difficult to evaluate, because there is much variation through time (FIGURES 9, 10, 11, 12). The only interesting observation we can make is that the greatest number of species in our samples occurs in SITE 1; this may be because it is the oldest secondary site, so, time [is] might be responsible for the greater accumulation of secondary species as it might also be for the increase of the number of species in SITE 3. But this interpretation should be confirmed because there is much variation and the number of samples made by us is not enough to give a completely satisfactory interpretation.

The temperature data of the four sites and of the germination house showed some differences (FIGURE 6) between the secondary and the primary sites, being more variable in the secondary locations. It is of interest that there is very little variation in soil temperature throughout the year. Nevertheless the temperature of a naked soil is very different from that of a vegetation-covered one (FIGURE 1), especially in the middle of

the day. We believe that this difference may explain the response of certain dormant seeds to the clearing of the forest. The temperatures in our germinating house were closer to those of a bare soil and the response we obtained from the plants was similar to that of an early colonized open soil.

CONCLUSIONS

The germination method is an effective one for evaluating the floristic potential of soils in tropical areas. In order to use it advantageously the composition of the flora and the ecology of the species of the region must be well known.

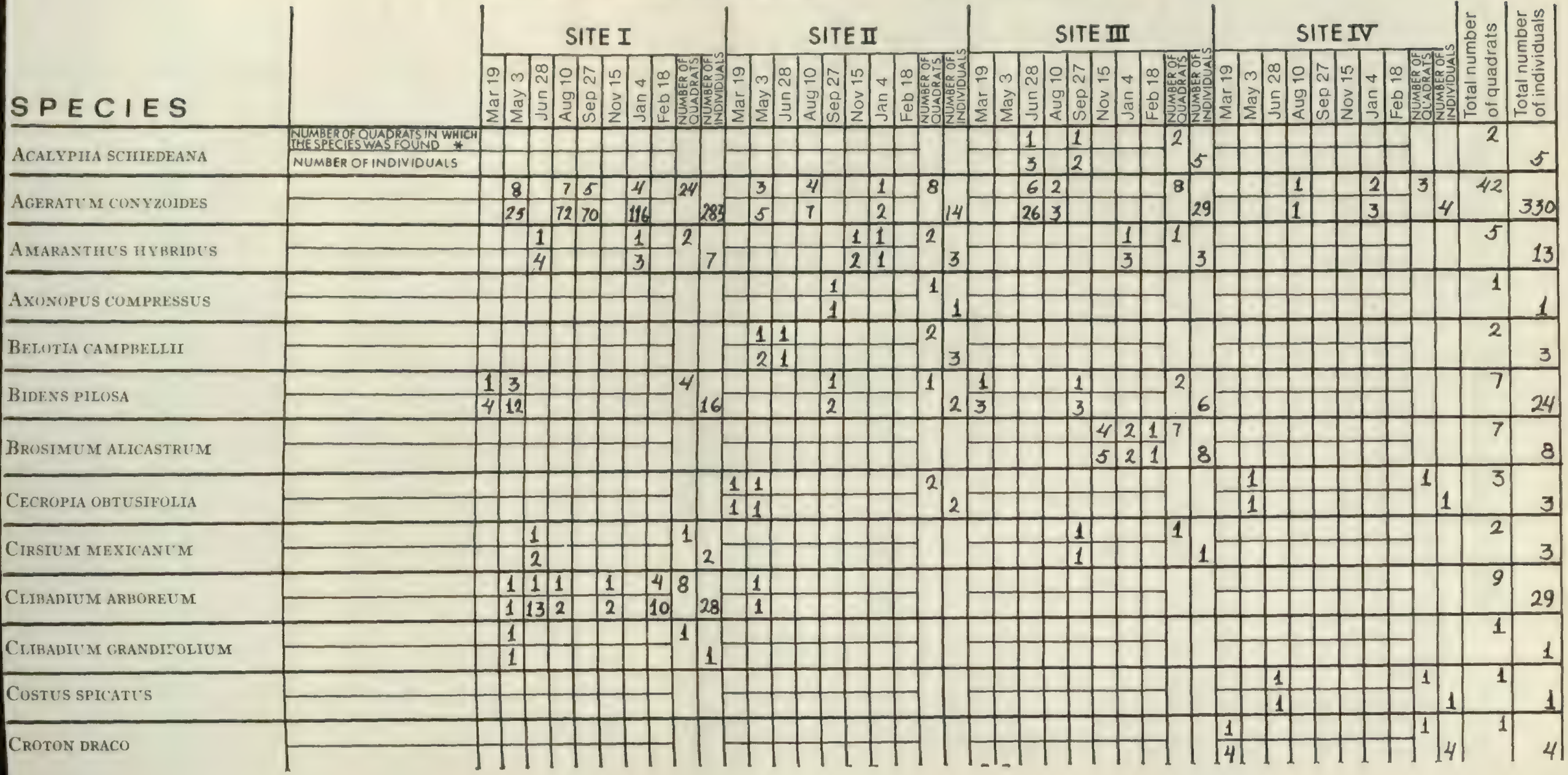
The greatest proportion of the seeds found in the soil of the four sites was comprised of seeds of secondary species, several of them being present through the year of the study, indicating that dormancy seems to be an important mechanism in the succession. No primary species showed that characteristic.

The initial stages of the succession are already imprinted in the soil of the primary selvas and its characteristics may be derived from other factors such as time of the initiation during the year and may also include effects of some chemicals, of temperature, fire, etc.

There are significant differences in the temperatures obtained in the primary sites compared with those of the secondary ones. But these data are difficult to evaluate in connection with the results obtained in this study. The thermoperiod may play an important role in the initial stages of the succession but this must still be proven.

More research should be done on comparable problems to reinforce some of the data obtained by us.

FIGURE 11. **Statistical data on the species found in the soil samples**



Desmodium adscendens																																						1	1		1	
																																						2		2		2
Dioscorea sp.		1							1																																1	
		2								2																																2
Emilia sonchifolia					1				1																																1	
					1					1																																1
Enterolobium cyclocarpum															1				1													1							1		2	
															1					1												1								1		2
Erechtites hieracifolia												1							1																						1	
												1								1																						1
Eupatorium sp.		1	10		6	5		8	30						4	3			7				5	2	4	1		3	15				2		4				6		58	
		2	60		65	120		160		387					5	6				11			25	3	6	1		30		65			2		14					16		479
Eupatorium macrophyllum												1							1			1			1				2												3	
												1								1		5			1					6												7
Eupatorium pansamalense																						1							1												1	
																						5								5												5
Eupatorium pycnocephalum															1				1																						1	
															2					2																						5
Euphorbia heterophylla		1							1																																1	
		1								1																																1
Heliocarpus appendiculatus																					1								1												1	
																					1									1												1
Heliocarpus aff. donnell-smithii				1		1			2		5	1						3	9							1	1		2			1							1		14	
				1		1				2	10	1						9		20						1	1			2		1								1		25
Iresine celosia	5	12	10	9	1	3	2	6	48		6	11	3	7	2	3	4	3	39		9	12	11	13	4	6	5	10	70		6	6	5	3			4	2	26		183	
	8	68	41	42	4	33	20	62		218	7	24	4	8	4	5	8	11		71	40	139	167	172	44	69	26	124		181	7	25	11	3			7	10		63		1193
Jacobinia sp.																						1							1												1	
																						2								2												2

FIGURE 11. **Statistical data on the species found in the soil samples**

SPECIES		SITE I										SITE II										SITE III										SITE IV											
		Mar 19	May 3	Jun 28	Aug 10	Sep 27	Nov 15	Jan 4	Feb 18	NUMBER OF QUADRATS	NUMBER OF INDIVIDUALS	Mar 19	May 3	Jun 28	Aug 10	Sep 27	Nov 15	Jan 4	Feb 18	NUMBER OF QUADRATS	NUMBER OF INDIVIDUALS	Mar 19	May 3	Jun 28	Aug 10	Sep 27	Nov 15	Jan 4	Feb 18	NUMBER OF QUADRATS	NUMBER OF INDIVIDUALS	Mar 19	May 3	Jun 28	Aug 10	Sep 27	Nov 15	Jan 4	Feb 18	NUMBER OF QUADRATS	NUMBER OF INDIVIDUALS	Total number of quadrats	Total number of individuals
LASIACIS PAPILLOSA	NUMBER OF QUADRATS IN WHICH THE SPECIES WAS FOUND *											1	1							2																						2	
	NUMBER OF INDIVIDUALS											1	1								2																							2
MIKANIA MICRANTHA									1	1																1	1		2	4												5	
									1		1															1	1		17		19												20
MIRABILIS JALAPA																	1			1																						1	
																	2				2																						2
NEUROLAENA LOBATA			1		1	1	1			4			1							1			1			1		1		3											8	
			1		1	1	1				4		1								1	1			1		1			3												8
PANICUM TRICHOIDES																1		1		2			1						1												3	
																2		1			3		1							1												4
PASPALUM SP.		1								1		1		1				1	1	4						1	1		2												7	
		3									3	1		1				1	2		5						1	2			3												11
PLEURANTHODENDRON MEXICANA																		1		1																						1	
																		3			3																						3
POTHOMORPHE UMBELLATA													3							3			1							1												4	
													6								6		1							1												7
PHYSALIS PUBESCENS																										1				1												1	
																										1				1												1
PHYTOLACCA DECANDRA		6				2	2	7	2	19		6	3	1	3	4		8	3	28		10	1		1	4	1	9	2	28		6	1	1	1	2	1	3	3	18		95	
		8				3	5	36	16		68	14	3	1	4	5		28	16		71	70	1		1	26	1	114	40		253	11	2	1	1	2	1	7	6		31		423
ROBINSONELLA MIRANDAE														1	1				5	7			5		2					7		1	7	7	9	2	7	8	9	50		64	
														1	2				15		18		5		5					10	2	17	17	19	2	12	15	25		108		137
SAPIUM LATERIFLORUM												1								1																						1	
												2									2																						2

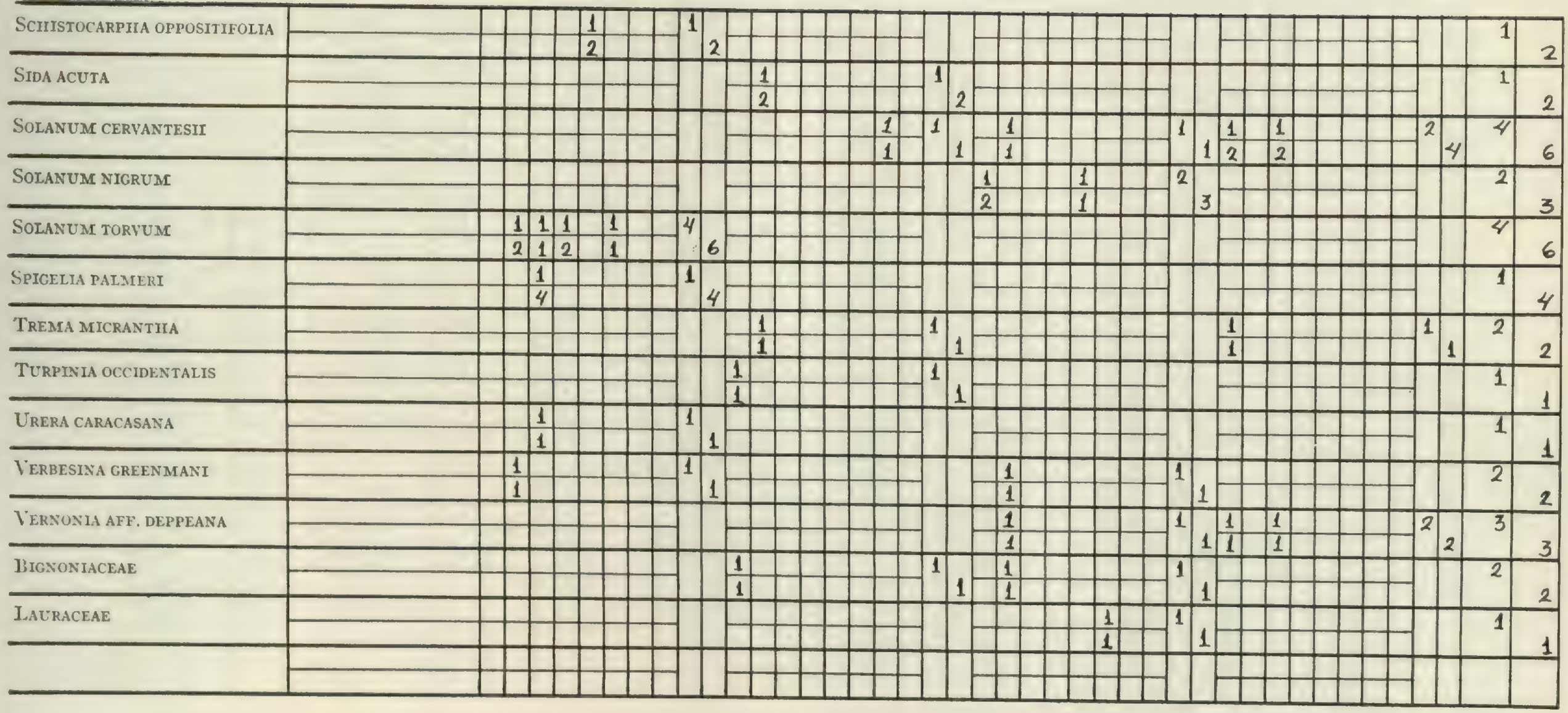

SCHISTOCARPHA OPPOSITIFOLIA
SIDA ACUTA
SOLANUM CERVANTESII
SOLANUM NIGRUM
SOLANUM TORVUM
SPIGELIA PALMERI
TREMA MICRANTHA
TURPINIA OCCIDENTALIS
URERA CARACASANA
VERBESINA GREENMANI
VERNONIA AFF. DEPPEANA
BIGNONIACEAE
LAURACEAE

FIGURE 12. **Seed content per m^2**

SEEDS PER M^2 12 CM. DEPTH	MAR 19	MAY 3	JUN 28	AUG 10	SEP 27	NOV 15	JAN 4	FER 18
SITE I	1982	3879	2937	3275	1982	4051	3189	3706
SITE II	517	862	344	603	431	431	862	862
SITE III	1120	1293	1439	1637	948	862	1560	2672
SITE IV	603	689	431	258	175	344	431	517

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FLORAL ANATOMY OF MYRTACEAE, II. EUGENIA

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UNTIL FAIRLY RECENTLY, the floral anatomy of the Myrtaceae had been a rather neglected area of botanical research (see Schmid, 1972c, for references to earlier work, especially those cited for Carr & Carr). Recent work on the *Eugenia-Syzygium* controversy (Schmid, 1971, 1972a–c) based the recognition of both taxa on new floral anatomical as well as on hitherto unemphasized organographic evidence. The bearing of floral anatomy on the taxonomy of the strictly Old World genus *Syzygium sensu lato* was the concern of a previous report (Schmid, 1972c), whereas the comparative floral anatomy of the mainly New World *Eugenia sensu stricto* (but including, for convenience, the Old World segregate *Jossinia*) is dealt with here.

MATERIALS AND METHODS

Reproductive material of three extra-American and 20 American species (including two varieties) of *Eugenia s. s.* was examined. TABLE I lists voucher specimens and other pertinent information for the species analyzed. Detailed methodology as well as reviews of the taxonomic and anatomical literature were given in earlier papers (Schmid, 1972b, c).

TABLE I: **Collection and preparation data for species studied** [1]

SPECIES, LOCALITY, COLLECTOR [2]	SECT.[3]	CLEARED [3] MTD.	CLEARED [3] UNMTD.
Eugenia acapulcensis Steud. MEXICO: Chiapas. *Breedlove 14490.*	4	0	0
— —. MEXICO: Michoacán. *McVaugh 22554.*	4	5	0
— —. NICARAGUA: Zelaya. *Standley 20016.*	5	0	0
Eugenia aeruginea DC. BRITISH HONDURAS. *Gentle 8073.*	4	0	0
— —. GUATEMALA: Petén. *Contreras 1403.*	0	3	6
— —. GUATEMALA: Petén. *Contreras 114.*	0	4	0
Eugenia biflora (L.) DC. BRAZIL: Pará. *Black 52–15623.*	2	4	0
— —. COLOMBIA: Vaupés. *Schultes & Cabrera 14236.*	1	6	0
— —. VENEZUELA: Bolívar. *Steyermark & Wurdack 31.*	3	4	0
— —. BRAZIL: Amapá. *Pires & Westra 48813.*	3	5	0
— —, var. *wallenii* (Macf.) Krug & Urban. JAMAICA. *Hart 1048.*	4	3	0
Eugenia capuli (Schlecht. & Cham.) Berg. MEXICO: Chiapas. *Breedlove 14407.*	5	12	4
— —. BRITISH HONDURAS. *Gentle 5044.*	6	2	6
Eugenia cartagensis Berg. COSTA RICA. *Austin Smith 77.*	6	5	0
Eugenia coffeifolia DC. LESSER ANTILLES: Guadeloupe. *L'Herminier s.n.*	9	0	0

— —. LESSER ANTILLES: St. Lucia. *Proctor 17978.*	2	7	0
Eugenia confusa DC. LESSER ANTILLES: St. Lucia. *Proctor 18135.*	3	0	0
— —. JAMAICA. *Proctor 23563.*	0	7	4
Eugenia duchassaingiana Berg. LESSER ANTILLES: Guadeloupe. *L'Herminier s.n.*	5	1	2
Eugenia flavescens DC. SURINAM. *Florschütz & Maas 2653.*	5	4	0
Eugenia florida DC. COLOMBIA: Amazonas. *Schultes & Cabrera 16236.*	6	0	0
— —. VENEZUELA: Bolívar. *Steyermark & Gibson 95781.*	0	4	0
Eugenia gregii (Sw.) Poir. LESSER ANTILLES: St. Lucia. *Proctor 18244.*	5	0	0
— —. LESSER ANTILLES: Martinique. *Hahn 641.*	0	2	2
Eugenia mandevillensis Urban. JAMAICA. *Proctor 26872.*	2	0	1
— —. JAMAICA. *Proctor 19686.*	3	1	2
Eugenia muricata DC. BRAZIL: Amapá. *Pires et al. 50887.*	7	2	2
Eugenia oerstediana Berg. MEXICO: San Luis Potosí. *King 4405.*	8	4	0
— —. BRITISH HONDURAS. *Gentle 2533.*	6	0	0
— —. MEXICO: Jalisco. *McVaugh 23418.*	4	5	0
Eugenia pleurocarpa Standl. MEXICO: Nayarit. *McVaugh 15322.*	7	7	1
Eugenia salamensis Donn. Sm. var. *hiraeifolia* (Standl.) McV. COSTA RICA. *Pittier 13952.*	5	0	0
— —, var. *salamensis*. MEXICO: Jalisco. *Carter & Chisaki 1209.*	3	4	0
Eugenia tikalana Lundell. GUATEMALA: Petén. *Contreras 1116.*	7	7	0
Eugenia uniflora L. BERMUDA. *Taylor 49–1048.*	4	5	0
— —. LESSER ANTILLES: Nevis. *Proctor 19469.*	0	3	0
Eugenia venezuelensis Berg. GUATEMALA: Petén. *Contreras 2971.*	4	5	0
Eugenia whytei Sprague in Stapf. LIBERIA. *Cooper 452.*	1	0	0
Eugenia winzerlingii Standl. GUATEMALA: Petén. *Contreras 1619.*	4	0	0
— —. MEXICO: Yucatán. *Lundell 851.*	0	8	0
— —. MEXICO: Yucatán. *Enriquez 815.*	0	2	0
Jossinia aherniana (C. B. Rob.) Merr. PHILIPPINES. *Velasco s.n.* (*Forestry Bureau 21779*).	4	1	0
Jossinia palumbis (Merr.) Diels. MARIANA ISLANDS. *Hosokawa 7570.*	2	0	0

[1] Voucher specimen of *Jossinia aherniana* at US (specimen courtesy Dr. R. H. Eyde), all others at MICH.

[2] Government administrative subdivisions (e.g., state, province, department, territory, etc.) given for larger countries only.

[3] Number of buds, flowers, and/or fruits sectioned (Sect.) and/or cleared. Columns under "Cleared" refer to number of items mounted (Mtd.) on permanent slides and unmounted (Unmtd.). All preparations from herbarium material.

OBSERVATIONS — GENERAL

Descriptions of the general organography, histology, and vasculature of *Eugenia s. l.* were presented in Schmid (1972b). Only the distinctive transeptal ovular supply of *Eugenia s. s.* is detailed below.

A variable number (up to about 11 per flower in my material) of bundles (placental strands) originate in several ways and constitute the transeptal ovular supply: (1) exclusively from the vascular cylinder of the floral tube (e.g., *Eugenia capuli*, FIGURE 13; *E. confusa*, FIGURE 1), (2) exclusively from a lateral carpellary system of various types (e.g., *E. flavescens*, FIGURE 18), (3) exclusively from the dorsal carpellary bundles (e.g., sometimes in *E. biflora*), or, usually (4) from any combination of the above. The mode and level of origin of the placental strands is by no means constant for a species or even an individual.

The placental strands enter the septum at different levels in the locular region and fuse variously (cf. FIGURES 3, 18, 19), eventually terminating at one or two centrally located placental plexuses. If a single placental plexus occurs, it may be a solid mass of vascular tissue (e.g., *Eugenia coffeifolia*, *E. tikalana*, *E. uniflora*, FIGURE 19) or it may be perforated by varying amounts of interfascicular parenchyma (e.g., *E. biflora*). As might be expected, these features are very variable within a species and in an individual.

There are at least three possible relationships between the dorsal carpellary bundles and the placental vascular system: (1) no connections as in *Eugenia capuli* (FIGURE 13), (2) occasional direct connections as in *E. confusa* (FIGURES 1, 3) or, usually (3) many indirect connections since a complex network of lateral carpellary bundles is interpolated between the dorsals and the placental vascular system, as in most species (e.g., *E. flavescens*, FIGURE 18). The presence or absence of an anastomosing lateral carpellary system is apparently not related to the size of the flower.

Many of these features of the transeptal ovular system are quite variable within a species or an individual. Nevertheless, it seems the ovarian vasculature of the species of *Eugenia s. s.* that I studied in detail can be broadly categorized as follows:

Dichotomous comparison of main types of ovarian vasculature in Eugenia s. s.

(1) Placental strands pendulous from near tops of loculi, the placental system (including strands and plexuses) thus appearing U- or V-shaped.

Placental strands on entering septum usually massive and often two, sometimes additional slender placental strands occurring; FLORIDA-type (FIGURE 15): e.g., *E. florida*, *E. biflora*, *E. coffeifolia*, *E. gregii*, *E. oerstediana*, *E. salamensis*.

(1) Placental strands entering sides of septum, the strands on entering septum usually slender.

(2) Placental strands usually few, with no connections to other carpellary vasculature (dorsal or lateral bundles); dorsal bundles also not connected to other carpellary bundles; CAPULI-type (FIGURE 13): e.g., ***E. capuli, E. venezuelensis.***

(2) Placental strands few to many, with connections to other carpellary vasculature; dorsal bundles also connected to other carpellary bundles.

(3) Dorsal bundles obscure; bundles to style several to often many (about 12); UNIFLORA-type (FIGURE 19): e.g., *E. uniflora.*

(3) Dorsal bundles readily definable; bundles to style two to several (to about 6); common.

(4) Placental strands usually few, with few connections to other carpellary vasculature, and these connections only to dorsal bundles; anastomosing carpellary system scanty or absent; CONFUSA-type (FIGURES 1, 3): e.g., *E. confusa, E. tikalana.*

(4) Placental strands often many, with few to many connections to dorsal and/or to lateral carpellary bundles, both of which generally form a simple to complex anastomosing system; FLAVESCENS-type (FIGURE 18): e.g., *E. flavescens, E. cartagensis, E. winzerlingii.*

EXPLANATION OF TABLE II: Floral structure of Eugenia s. s. and Jossinia

The abbreviations at the head of each column correspond to the following taxa: Bif A, *Eugenia biflora, Pires & Westra 48813* (MICH); Bif B, *E. biflora, Black 52–15623* (MICH); Bif C, *E. biflora, Schultes & Cabrera 14236* (MICH); Cap, *E. capuli*; Car, *E. cartagensis*; Cof, *E. coffeifolia*; Con, *E. confusa*; Fla, *E. flavescens*; Flo, *E. florida*; Oer, *E. oerstediana*; Sal s, *E. salamensis* var. *salamensis*; Sal h, *E. salamensis* var. *hiraeifolia*; Tik, *E. tikalana*; Uni, *E. uniflora*; Ven, *E. venezuelensis*; Win, *E. winzerlingii*; Jos, *Jossinia aherniana.*

CHARACTER 1. The maximum size of the bud near anthesis, width (at widest part of perianth) times length (base to tip of bud), was determined from sectioned or cleared material. This creates a bias toward smaller buds since these are often selected for easier manipulation and study. Maximum dimensions as indicated in the taxonomic literature are often much greater.

CHARACTER 2. The maximum prolongation of the floral tube above the ovary was determined according to taxonomic criteria. Such measurements, however, may include some ovarian tissue due to the top of the ovary being depressed (see Schmid, 1972b).

CHARACTER 5. The amount of pubescence was graded as follows: glabrous, essentially glabrous, little, or much.

CHARACTER 6. The vasculature of other floral parts is also invariably closed.

CHARACTER 7. See Schmid (1972b) for definition of terms.

CHARACTER 8. Minor bundles in some species are more or less uniformly dispersed throughout tissue of floral tube in the locular region of flower.

CHARACTER 10. The major bundles usually branch distally.

CHARACTER 11. See text for descriptions of types of ovarian vasculature.

CHARACTER 12. This includes all carpellary vasculature (except dorsal bundles) in locular region.

TABLE II. **Features of floral structure of Eugenia s. s. and Jossinia ***

CHARACTER	*Bif* A	*Bif* B	*Bif* C	*Cap*	*Car*	*Cof*	*Con*	*Fla*	*Flo*	*Oer*	*Sal s*	*Sal h*	*Tik*	*Uni*	*Ven*	*Win*	*Jos*
ORGANOGRAPHY																	
(1) Maximum size bud	4.0×	3.5×	1.8×	1.7×	2.3×	2.2×	2.7×	2.6×	2.5×	2.7×	3.8×	3.8×	1.6×	3.0×	1.6×	3.5×	5.4×
(mm. width × length)	6.2	5.3	2.8	2.2	3.7	3.0	4.1	4.5	3.6	3.9	5.0	5.2	2.0	5.0	1.8	5.0	7.5
(2) Max FT prolonged (mm.)	.4	.5	.7	0	.25	0	.6	0	.4	.4	.2	1.1	0	.5	0	.1	1.3?
HISTOLOGY																	
(3) Scleren in flower	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
(4) Scleren in pedicel	—	—	—	—	+	dna	—	—	X	—	—	—	—	+	—	+	dna
(5) Amount pubescence fl	m	m	m	li	g	li(m)	g	g	eg(m)	eg	m	m	li	g(eg)	li	g	m
VASCULATURE FT																	
(6) Vasc open or closed	cl	cl	cl	cl	cl	cl	cl	cl	cl	cl	cl	cl	cl	cl	cl	cl	cl
(7) Mono- or zonocyclic	mono	mono	mono	mono	mono	mono	mono	mono	mono	mono	mono	mono	mono	mono	mono	mono	mono
(8) Minor VBs diffused	—	—	—	—	—	—	—	—	+	+	—	+	—	—	—	—	+
(9) Amount minor vasc	m	m	m	li	m	li	m	m	m	m	m	m	li	m	li	m	m
(10) # MBs at base	8(9)	8	8?	8	8,10	8	8	8	8	8(9)	8	8(–10?)	8	8	8	8	8

	Vasculature Ovary																	
(11)	Type	flo	flo	X	cap	fla	flo	con	fla	flo	flo	flo	flo	con	uni	cap	fla	dna
(12)	Amount VT by loculi	li	v li	v v li	v li	li	m	li	m	m	m	m	m	v li	m	v li	li	v v m
(13)	Anastomoses in LCV	+	+	–	–	+	+	–	+	+	+	+	+	–	+	–	+	+(v m)
(14)	DCBs connected to other carpellary VT	+	+	–	–	+	+	+	+	+	+	+	+	+	dna	–	+	dna
	Vasculature Style																	
(15)	# VBs at base	2(3)	2	2	2	2(3)	2	2(3)	2	3–5	3–6	2	2	2	5–12	2	3(2,4)	3–5
(16)	SVBs extension of both DCBs	+	+	+	+	+	+	+	+	+	+	+	+	+	dna	+	+	dna
(17)	SVBs extension of LCBs	occ	–	–	–	occ	–	occ	–	+	+	–	–	–	+	–	u	+
(18)	SVBs branched	–	–	–	occ	+	occ	occ	+	u	+	+	–	–	+	–	+	+
(19)	VT to tip	+	+	+	+	+	+	+	+	+	+	+	+	+	+	nearly	+	+
(20)	VT at tip expanded	+	+	+	u	+	+	+	u	+	+	+	–	+	+	–	+	X

* See preceding page for explanation of characters and abbreviations of names of taxa.

Symbols and Abbreviations: The following are used, without punctuation, to shorten entries: **X**, could not be determined from my material; +, present or yes; –, absent or no; **cap**, capuli-type; **cl**, closed; **con**, confusa-type; **DCBs**, dorsal carpellary bundles; **dna**, does not apply; **eg**, essentially glabrous; **fl**, flower; **fla**, flavescens-type; **flo**, florida-type; **FT**, floral tube; **g**, glabrous; **li**, little; **LCBs**, lateral carpellary bundles; **LCV**, lateral carpellary vasculature; **m**, many, much; **max**, maximum; **MBs**, major vascular bundles; **occ**, occasionally; **scleren**, sclerenchyma; **SVBs**, stylar vascular bundles; **u**, usually; **uni**, uniflora-type; **v**, very; **vasc**, vasculature; **VBs**, vascular bundles; **VT**, vascular tissue.

These types of ovarian vasculature are typological and do not necessarily indicate relationships since several patterns seem of general occurrence in the genus.

OBSERVATIONS — INDIVIDUAL SPECIES

Much repetitive descriptive information for the species of *Eugenia s. s.* investigated is relegated to TABLE II. Detailed descriptions are given for *E. biflora*, *E. capuli*, and *E. confusa*. Reference should be made both to the tables and to the species descriptions for a complete profile of any one species. The account for each species is based on all the specimens examined (see TABLE I) and represents a range of variability for one or more specimens (individuals) of that species.

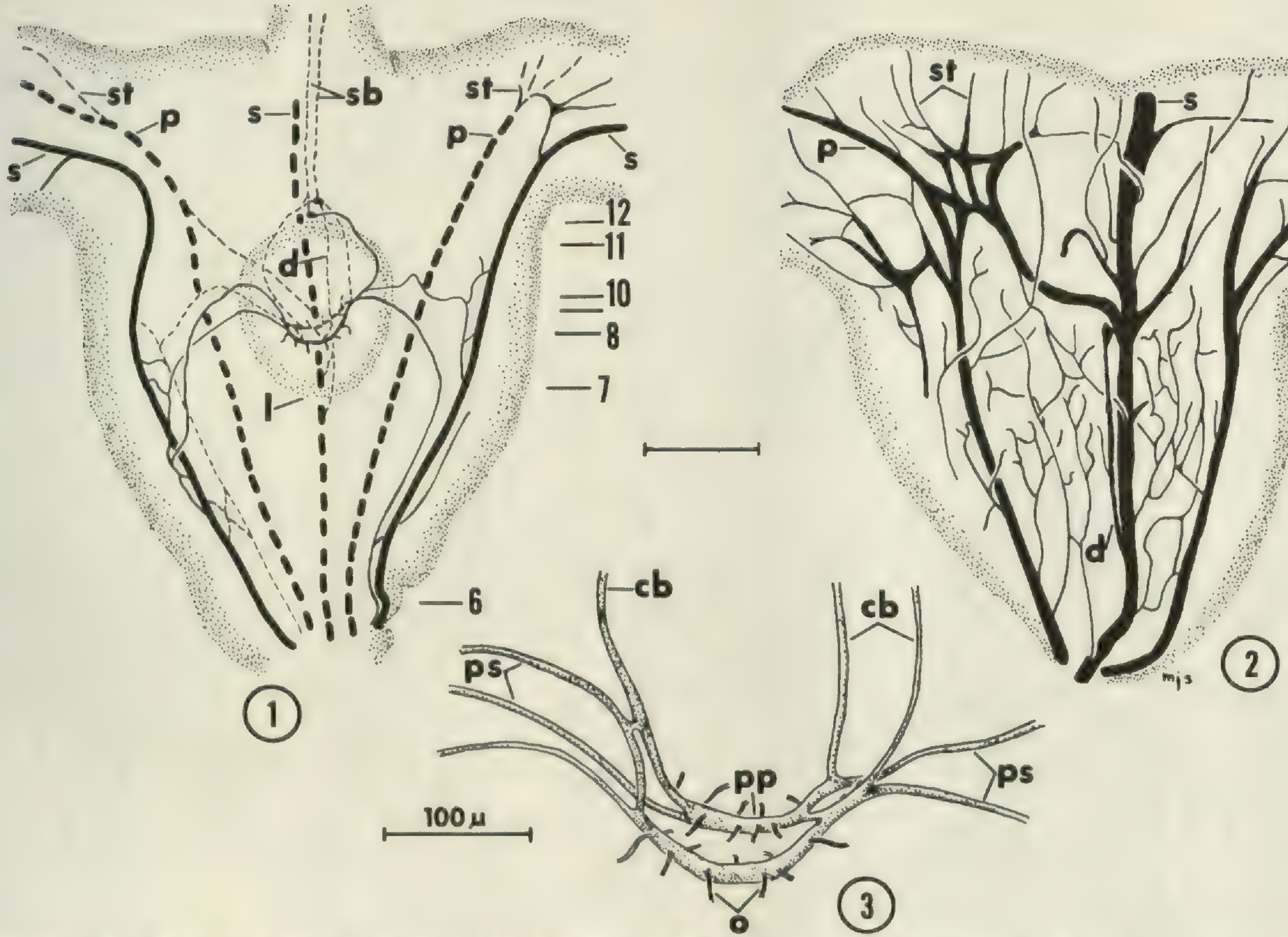
Organographic and histological data were not heavily emphasized since their apparent minor taxonomic usefulness in a small survey such as mine did not justify the labor involved in their compilation. Detailed study of a number of taxa revealed that several features of vasculature exhibit much variability. Hence, a number of vascular characters examined for *Syzygium s. l.* (see Schmid, 1972c) were not studied in detail for many species of *Eugenia s. s.* For example, the level and nature of origin of the dorsal carpellary bundles were not determined for many taxa of *Eugenia s. s.* since these features are very variable and difficult to define, much more so than in *Syzygium s. l.* (see Schmid, 1972a, c). The vascular characters given in TABLE II were selected as the most promising for comparative purposes.

The arrangement of the 13 American species examined in the greatest detail is essentially according to similarity of ovarian vasculature, based on the five types described above. Taxa were designated as exemplifying a particular type of ovarian vasculature chiefly because clearings of excellent quality were available for three-dimensional reconstructions. Comparisons between patterns of vasculature of the floral tube, ovary, and style are not necessarily indicative of relationships since several patterns seem of general occurrence in the genus (as noted above).

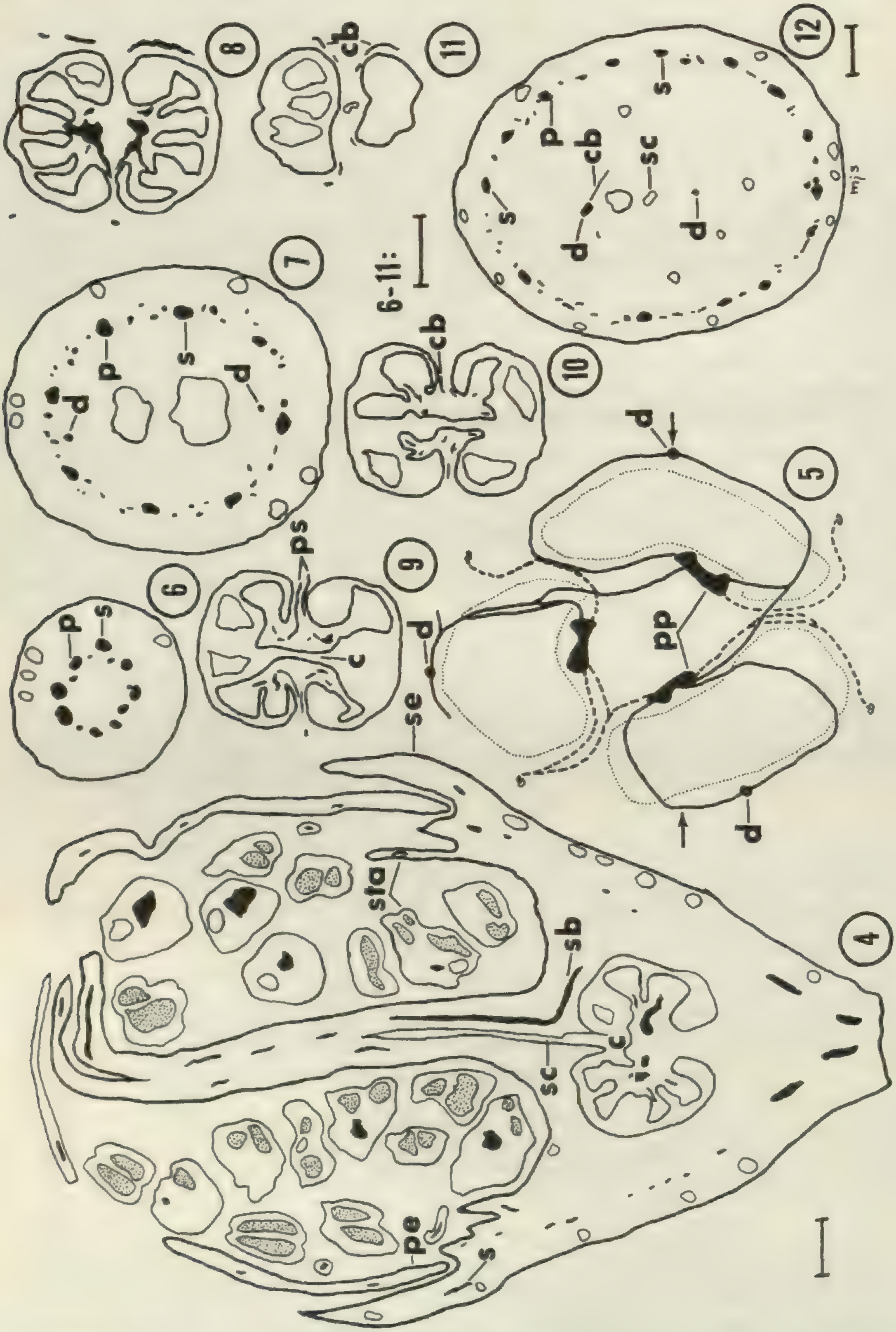
Eugenia confusa DC.

For synonymy see Urban (1895). The two plants examined are anatomically very similar.

VASCULATURE. See TABLE II. A single, unbranched bundle extends to the tip of each of the two bracteoles subtending the flower. The floral vasculature forms a closed system. Eight discrete major bundles comprise the vascular cylinder in the base of the flower (FIGURES 1, 2, 6). Throughout the extent of the floral tube, these eight bundles exhibit a monocyclic arrangement (defined in Schmid, 1972b) and frequently branch, producing mostly small minor strands that anastomose profusely in a very irregular pattern (FIGURES 2, 6, 7, 12). Distally, the eight major bundles, which usually extend into the eight perianth parts, branch extensively in an irreg-



FIGURES 1–3. **Eugenia confusa** (*Proctor 23563*, MICH). FIGURES 1, 2, Reconstruction of part and counterpart of a cleared flower cut in plane of septum between the two carpels. Minor vasculature omitted from FIGURE 1, vasculature of FIGURE 2 complete. Numerals at edge of FIGURE 1 indicate approximate levels of transections shown in FIGURES 6–12. FIGURE 3, Enlargement of FIGURE 1 showing placental system formed by five placental strands and three central axis bundles. ABBREVIATIONS: cb, central axis bundle; d, dorsal carpellary bundle; l, limits of ovarian locule; o, ovular trace; p, petal bundle; pp, placental plexus; ps, placental strand; s, sepal bundle; sb, stylar bundle; st, stamen trace. Unlabeled magnification bar equals 250 μ.



FIGURES 4–12. **Eugenia confusa** (*Proctor 18135*, MICH). FIGURE 4. Longisection of anomalous tricarpellate flower cut in plane indicated by arrows in FIGURE 5. FIGURE 5. Transectional reconstruction of flower in FIGURE 4, representing telescoped view of placental region. Dashed lines indicate placental strands at levels mainly below the three placental plexuses; solid lines indicate central axis bundles at levels above placental plexuses. Outlines of loculi (dotted lines) correspond to level of placental plexuses; compitum and outlines of

ular manner and supply narrow traces to the stamens and generally thicker strands to the perianth segments (FIGURES 1, 2).

The ovarian vasculature exemplifies the CONFUSA-type (FIGURES 1, 3). It is complex and exceedingly variable, much more so than originally thought (Schmid, 1970). The several placental strands originate from various sources in the vascular cylinder of the floral tube, that is, directly from a major bundle or more typically from the anastomosing strands produced by the major bundles (FIGURES 1, 8). In addition, they originate at various levels in the flower, from near its base to within the placental region (FIGURE 1). As they ascend and traverse the tissue next to the loculi, the placental strands occasionally produce short branches, but eventually the former enter the middle part of the septum, turn downward, and terminate at two placental plexuses (FIGURES 1, 3, 5, 8, 9). Each placental plexus is usually formed by the fusion and subsequent proliferation of the placental strands of the same carpel (FIGURES 3, 5, 8). There is generally little contact between the placental strands of adjacent carpels, although these strands do come very close together in the septum (FIGURES 5, 8, 9). Several bundles, designated central axis bundles, extend from the four corners of the placental system and connect with the two dorsal carpellary bundles near the tops of the loculi (FIGURES 3, 5, 10–12). FIGURE 5, based on an atypically tricarpellate flower, illustrates the variability of vasculature in the placental region.

The two dorsal carpellary bundles usually originate below the loculi and occasionally produce short branches that terminate in the ovary (FIGURES 1, 2, 7). The dorsals, sometimes accompanied by a third strand, vascularize the style (FIGURES 1, 4). The stylar bundles generally do not branch, but expand near the tip of the style (FIGURES 1, 4).

Eugenia capuli (Schlecht. & Cham.) Berg

Synonyms include *Myrtus capuli* Schlecht. & Cham. and *Eugenia contrerasii* Lundell (see McVaugh, 1963a, b). The only difference detected between the two collections I studied was that the stylar bundles of one specimen (*Breedlove 14407*) were distally expanded and occasionally branched whereas those of the other (*Gentle 5044*) were not. The latter collection had been identified as *E. contrerasii* Lundell. The fact that the two collections are so very similar anatomically supports McVaugh's (1963a, b) inclusion of *E. contrerasii* in the synonymy of *E. capuli*.

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loculi at other levels not indicated. FIGURES 6–12, Transections of flower taken from levels indicated in FIGURE 1. Only locular portions of flowers are shown in FIGURES 8–11 since outer vasculature is similar. FIGURE 7 is above level of origin of dorsal carpellary bundles, these omitted from FIGURES 8–11. In FIGURES 6, 7, and 12 the eight largest bundles correspond to the major bundles. four sepal bundles alternating with four petal bundles. ABBREVIATIONS: c, compitum; cb, central axis bundle; d, dorsal carpellary bundle; p, petal bundle; pe, petal; pp, placental plexus; ps, placental strand; s, sepal bundle; sb, stylar bundle; sc, stylar canal; se, sepal; sta, stamen. Magnification bars equal 250 μ.

HISTOLOGY. The floral tube and sepals are puberulent (see Schmid, 1972b, *Figures 1, 2*).

VASCULATURE. See TABLE II. A single, unbranched bundle extends to the tip of each of the two nearly contiguous bracteoles. The vasculature of the flower forms a closed system. Eight discrete major bundles occur in the tip of the pedicel and the base of the flower (FIGURE 13). In contrast to *Eugenia confusa* (FIGURE 2), these eight major bundles produce relatively few minor, anastomosing strands throughout the extent of the floral tube (FIGURE 13). Distally, the eight major bundles divide profusely in an irregular manner and supply strands to the four sepals, the four petals, or the many stamens (FIGURE 13).

The ovarian vasculature exemplifies the CAPULI-type (FIGURE 13). Originating either directly from a major bundle or generally from anastomoses produced by the major bundles, a variable number of placental strands arise at various levels in the flower and enter the ovarian tissue (FIGURE 13). At the ends of the septum, these placental strands fuse into two compound placental strands that traverse the septum. The placental vasculature usually does not exhibit the arching pattern characteristic of *Eugenia confusa*. In the center of the ovary, the two compound placental strands each divide and form two placental plexuses. The vascular tissue in the placentae thus displays a diamond-shaped pattern, with a parenchymatous core (FIGURE 13). There are no vascular connections between the placental vascular system and the dorsal carpellary bundles, unlike the situation in *E. confusa*.

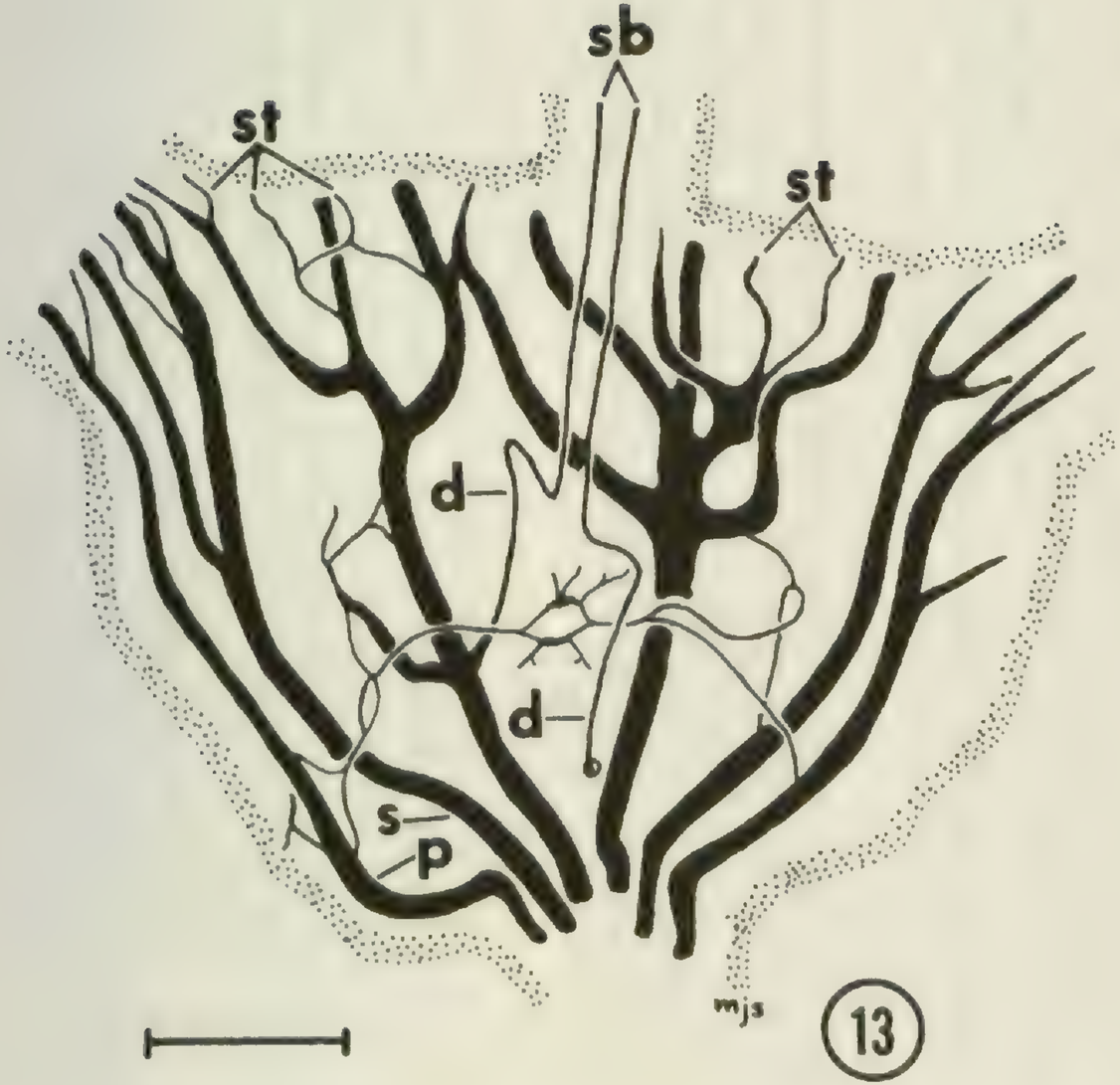
The level and manner of origin of the two dorsal bundles is very variable. The dorsals usually originate in the locular region, but they may arise anywhere from just above the loculi to near the junction of the pedicel and flower. In addition, each dorsal originates either directly from a major bundle or sometimes from several anastomosing strands produced by one or more major bundles. The dorsals do not branch in the ovary and only occasionally, distally, in the style (FIGURE 13). The bundles usually expand near the tip of the style.

Eugenia tikalana Lundell

McVaugh (1963b, p. 366) remarked that "this species is superficially almost indistinguishable from *E. capuli*." Anatomically, the two species are also very similar, *E. tikalana* differing only in its gynoecial vasculature (TABLE II, characters 11 and 14), which is of the CONFUSA-type (FIGURES 1, 3). In *E. tikalana* several placental strands enter the sides of the septum and terminate at a single placental plexus (FIGURE 14). There are usually a few vascular connections between the placental system and the dorsal carpellary bundles, as in *E. confusa*.

Eugenia venezuelensis Berg

Synonyms include *Eugenia origanoides* Berg. The name usually used is *E. origanoides* (see McVaugh, 1958, 1963a, b, for full description and



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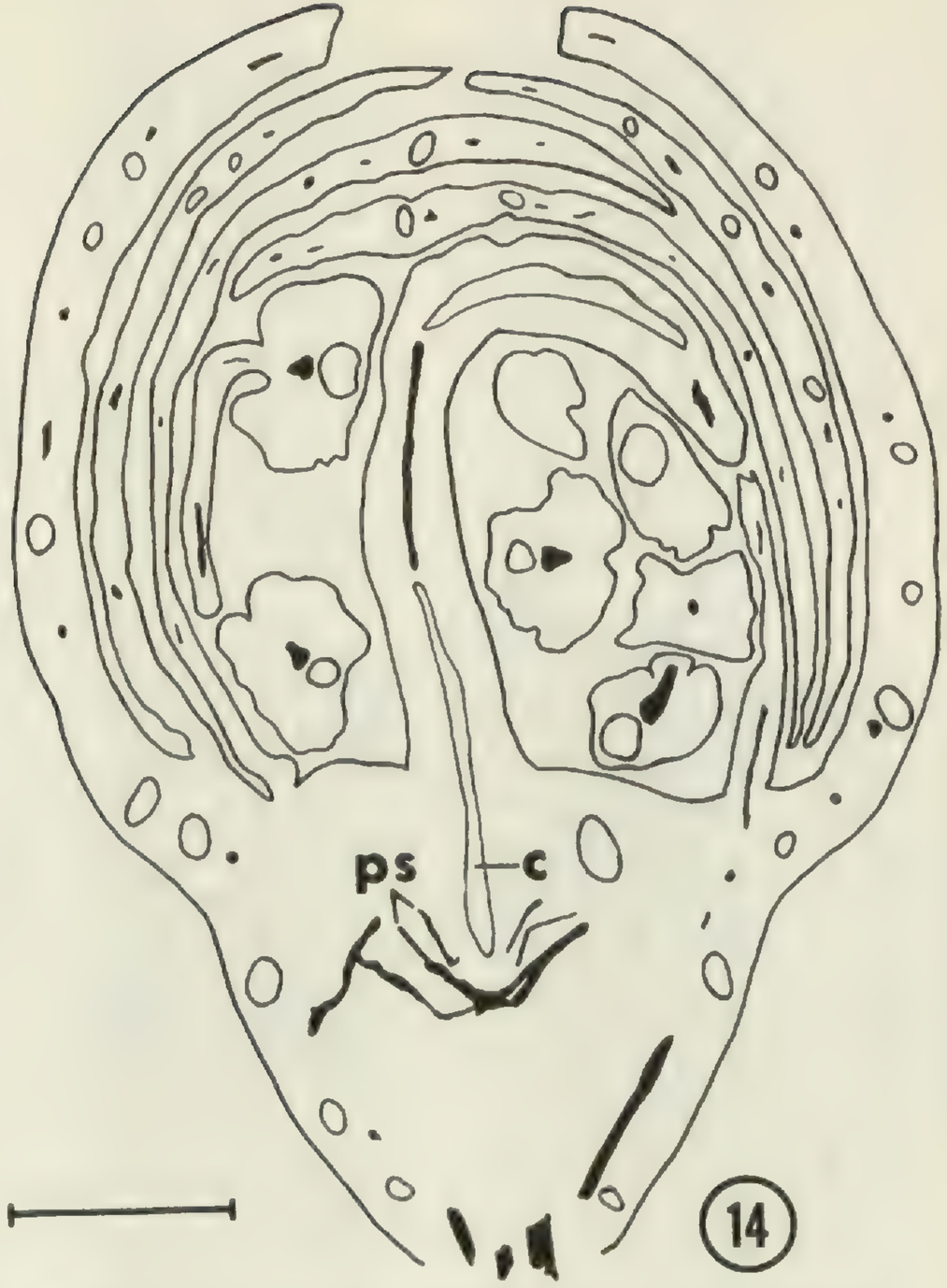

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FIGURES 13 and 14. FIGURE 13, **Eugenia capuli** (*Breedlove 14407*, MICH). Reconstruction of cleared flower. Minor vasculature and part of flower with two major bundles omitted for clarity. Ovarian loculi not indicated. Four sepal bundles alternate with four petal bundles. FIGURE 14, **Eugenia tikalana.** Longisection of flower cut in plane of septum, showing central placental plexus. ABBREVIATIONS: c, compitum; d, dorsal carpellary bundle; p, petal bundle; ps, placental strand; s, sepal bundle; sb, stylar bundle; st, stamen trace. Magnification bars equal 250 μ and 310 μ respectively.

synonymy). However, McVaugh informs me (1971) that he saw the type of *E. venezuelensis* and it is the same as that of *E. origanoides*.

Eugenia venezuelensis is distinguished from *E. capuli* or *E. tikalana* chiefly by its more abundant and conspicuous pubescence (McVaugh, 1963a, b), but the hairs of the three species are of very similar morphology (as in Schmid, 1972b, *Figures 1, 2*). Anatomically, the three species are very similar (see TABLE II) although the placental vasculature of *E. venezuelensis* more closely resembles that of *E. capuli* (FIGURE 13).

VASCULATURE. See TABLE II. At each end of the septum two placental strands fuse into a compound strand that terminates at a single placental plexus. The two stylar bundles, which end as far as 210 microns from the stigma, terminate further from the stigma than do the stylar bundles of other species of *Eugenia s. s.* examined. The delicate vascular strand (one or two vessel elements thick) of the filament expands considerably (over 10 times) in the connective and abuts against a terminal secretory cavity that is up to 110 microns in dimension. The staminal vasculature of *E. capuli* and *E. tikalana* is very similar.

Eugenia florida DC.

For synonymy see McVaugh (1958, 1969). The two collections I examined are anatomically very similar. See also remarks under *Eugenia oerstediana*.

HISTOLOGY. The sepals are ciliate (see Schmid, 1972b, *Figure 5*), and strigose chiefly within (see Schmid, 1972b, *Figures 3, 4*). One collection (*Steyermark & Gibson 95781*) has a very pubescent floral tube and staminal disc (see Schmid, 1972b, *Figures 3, 4*).

VASCULATURE. See TABLE II. The non-gynoecial vasculature is like that of *Eugenia biflora* (see TABLE II; FIGURES 16, 17). A chief difference is that in *E. florida* there are numerous tiny bundles between the loculi and the vascular cylinder of the floral tube.

The ovarian vasculature exemplifies the FLORIDA-type (FIGURE 15). Near the bottoms of the loculi many minor carpellary bundles bend inward from the innermost part of the floral tube, become arranged in a ring with the two dorsal carpellary bundles, and distally anastomose with each other and with the dorsals (FIGURE 15). Two (usually) massive placental strands originate from this anastomosing system just above the loculi and descend in opposite ends of the septum to the two placental plexuses (FIGURE 15). However, unlike other species which have the FLORIDA-type of ovarian vasculature, in *Eugenia florida* there are no additional slender placental strands entering at lower levels. Above the loculi the two dorsals and a variable number of other bundles (some containing only unlignified elements) often fuse with each other before entering the style (FIGURE 15).

Eugenia oerstediana Berg

Synonyms include *Eugenia vincentina* Krug & Urban ex Urban, *E. conzattii* Standl., *E. cocquericotensis* Lundell, *E. petenensis* Lundell, and

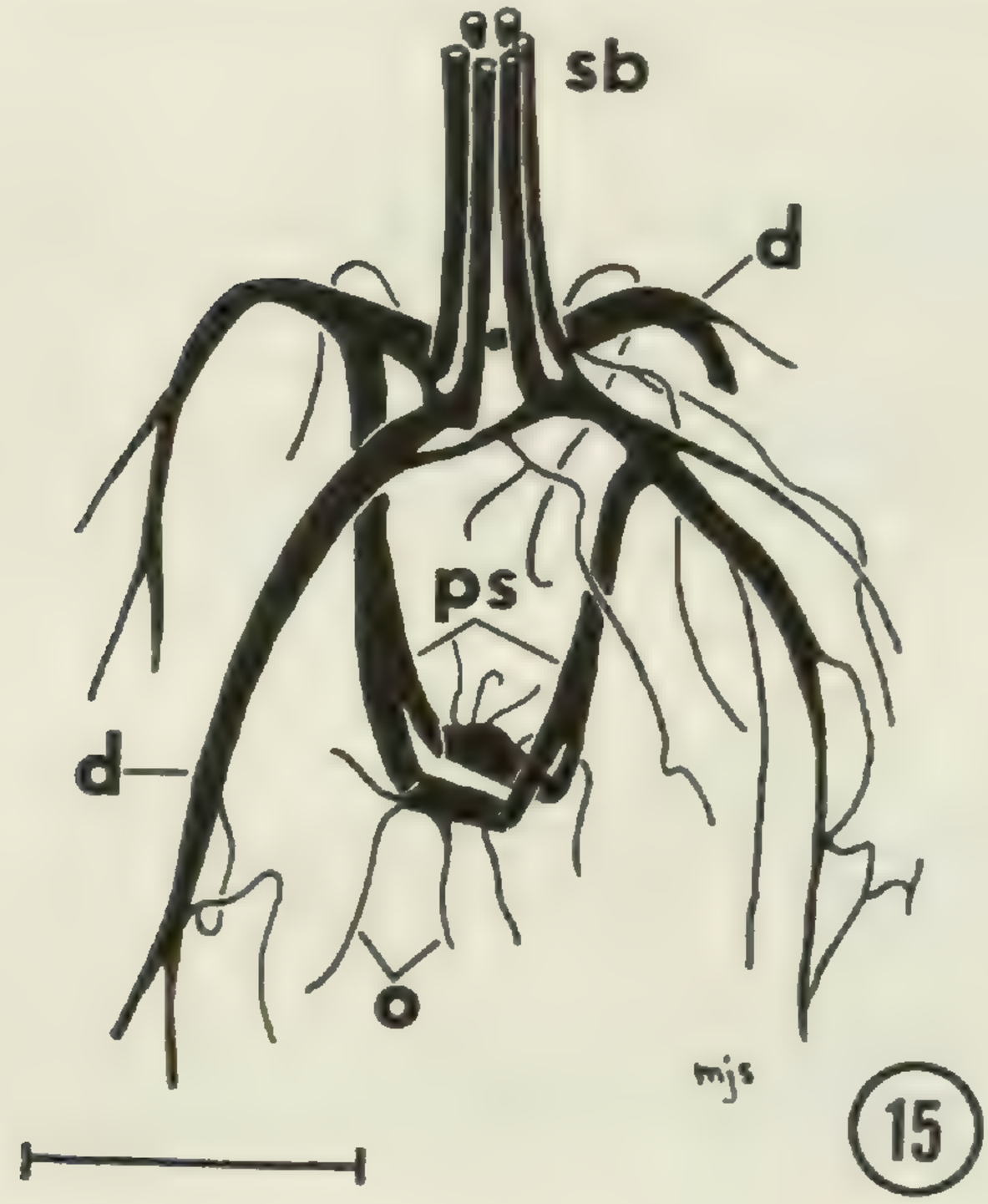


FIGURE 15. **Eugenia florida** (*Steyermark & Gibson 95781*, MICH). Reconstruction of placental system and associated carpellary vasculature. Two placental plexuses are present. Outlines of ovarian loculi and some minor vasculature omitted. ABBREVIATIONS: d, dorsal carpellary bundle; o, ovular trace; ps, placental strand; sb, stylar bundle. Magnification bar equals 250 μ.

E. eutenuipes Lundell (see McVaugh, 1963a, b). It should be noted that Berg's (1855–56) *E. oerstedeana* is an orthographic error for *E. oerstediana*.

Of the three collections sampled, one had been identified as *Eugenia oerstediana* (*McVaugh 23418*), another as *E. conzattii* (*King 4405*), a third as *E. cocquericotensis* (*Gentle 2533*). McVaugh (1963a, b) considered the latter two names to be synonyms of the former. Floral anatomy supports this treatment since all three collections are very similar. Any two flowers, either from the same plant or from two different collections, may vary in a few very subtle respects, but analysis of a total of 27 flowers for the three collections indicates most such variations merely represent different points on a morphocline. *Gentle 2533*, however, differs slightly and consistently from the other two collections, chiefly in having (1) the dorsal carpellary bundles only weakly connected to the other carpellary bundles and (2) the two massive placental strands attached usually just below (as opposed to just above) the tops of the loculi. *King 4405* differs from the other two collections in having (1) an extremely short floral tube (.1 mm. versus .3–.4 mm.), (2) very many tiny bundles occurring between the loculi and the vascular cylinder of the floral tube, and (3) the minor carpellary bundles occurring further from the loculi than do comparable carpellary bundles of the other collections. *Gentle 2533* and *King 4405* both differ from *McVaugh 23418*

in having, respectively, four and six (rather than a variable number) strands at the base of the style.

Taxonomically, *Eugenia oerstediana* appears to be closely allied to *E. florida* (McVaugh, 1963a, b, 1969) and perhaps derived from it (McVaugh, 1963a). McVaugh (1963a, p. 448) questioned "the propriety of recognizing *E. oerstediana* as a species distinct from *E. florida*" since the two are "virtually indistinguishable" except in ovule number and in characters of the inflorescence and pedicel. Anatomically, my three collections of *E. oerstediana* are exceptionally similar to my two collections of *E. florida* (see TABLE II). The only consistent difference I found between the two species is that the placental strands in *E. florida* are attached at a slightly higher level so that the placental system in side view appears more U-shaped, with nearly vertical placental strands (FIGURE 15), whereas that of *E. oerstediana* appears V-shaped, with sloping placental strands. One collection of *E. oerstediana* (*McVaugh 23418*), in particular, is anatomically nearly indistinguishable from *E. florida*. It seems, then, that *E. florida* is best regarded as a widely distributed complex comprised of such scarcely distinguishable forms as *E. oerstediana*, *E. conzattii*, and *E. cocquericotensis*, to mention just the species for which anatomical evidence is now available.

HISTOLOGY. Only the sepals are pubescent (ciliate, with hairs like those in Schmid, 1972b, *Figure 1*).

VASCULATURE. See TABLE II. As explained above, the vasculature is very close to that of *Eugenia florida*.

Eugenia biflora (L.) DC.

McVaugh (1958, 1969) and Urban (1895) give extensive synonymy. I examined five collections for *Eugenia biflora* (see TABLE I). Since these are rather dissimilar, there are three entries for this species in TABLE II, as explained below.

One collection (*Black 52–15623*), listed separately in TABLE II as *Eugenia biflora* "B", differs considerably from the other four collections (see also TABLE II), viz.: Although the ovarian vasculature is of the FLORIDA-type (FIGURE 15), the pendulous placental strands are rather narrow, and there are very few connections between the dorsal bundles and other carpellary bundles. *Black 52–15623* also differs from the other collections in some less important respects: (1) Its staining properties are very different. (2) Much of the septum is often very thin, consisting of one to three layers of cells.

A second collection (*Schultes & Cabrera 14236*) is even more different and thus is also listed separately in TABLE II (as *Eugenia biflora* "C"). Differences from the other collections studied include the following: (1) Only four (as opposed to many) ovules are present per flower. (2) The number of major bundles is difficult to determine since these branch repeatedly throughout the floral tube. The relationship between the vasculature of the floral tube and that of the perianth parts is therefore ob-

scure. (3) Only one strand enters each sepal, but more than one supplies each petal. (4) The ovarian vasculature is quite unlike that of the other collections examined, but I cannot detail how it differs as my preparations are of poor quality. (5) The lateral carpellary system is only weakly developed, with apparently no anastomoses or connections to the dorsal bundles.

The three other collections (*Hart 1048*; *Pires & Westra 48813*; *Steyermark & Wurdack 31*), designated *Eugenia biflora* "A", are very similar, particularly in their vasculature. The entry *E. biflora* "A" in TABLE II is based on *Pires & Westra 48813*, which was studied in the greatest detail. These three collections differ chiefly as follows: (1) The maximum prolongation of the floral tube above the ovary was 0 mm. and .6 mm. for *Hart 1048* and *Steyermark & Wurdack 31*, respectively. (2) In *Pires & Westra 48813* usually only the two dorsal carpellary bundles continue to the tip of the style, but in the other two collections the two dorsals are often accompanied into the style by additional carpellary bundles.

Ranging from southern Mexico and the West Indies to Bolivia and northern Brazil (McVaugh, 1963b, 1969), *Eugenia biflora* is "probably the most widespread, and certainly the most variable, of any native [American] species of the family" (McVaugh, 1969, p. 167; see also McVaugh, 1958). The four South American collections I examined (see TABLE I) are cited under *E. biflora* by McVaugh (1969) in his most recent work on the Myrtaceae. At my request, McVaugh reëxamined (August, 1971) the collections designated here as *E. biflora* "B" and "C", but he still thinks they are good *E. biflora*. In view of the notorious variability of this species, it is not surprising that *E. biflora* "A", "B", and "C" differ markedly (see TABLE II, which does not do justice to the differences between "A", "B", and "C"). However, perhaps these differences are no more significant than those evident between *E. salamensis* varieties *salamensis* and *hiraeifolia* (see TABLE II).

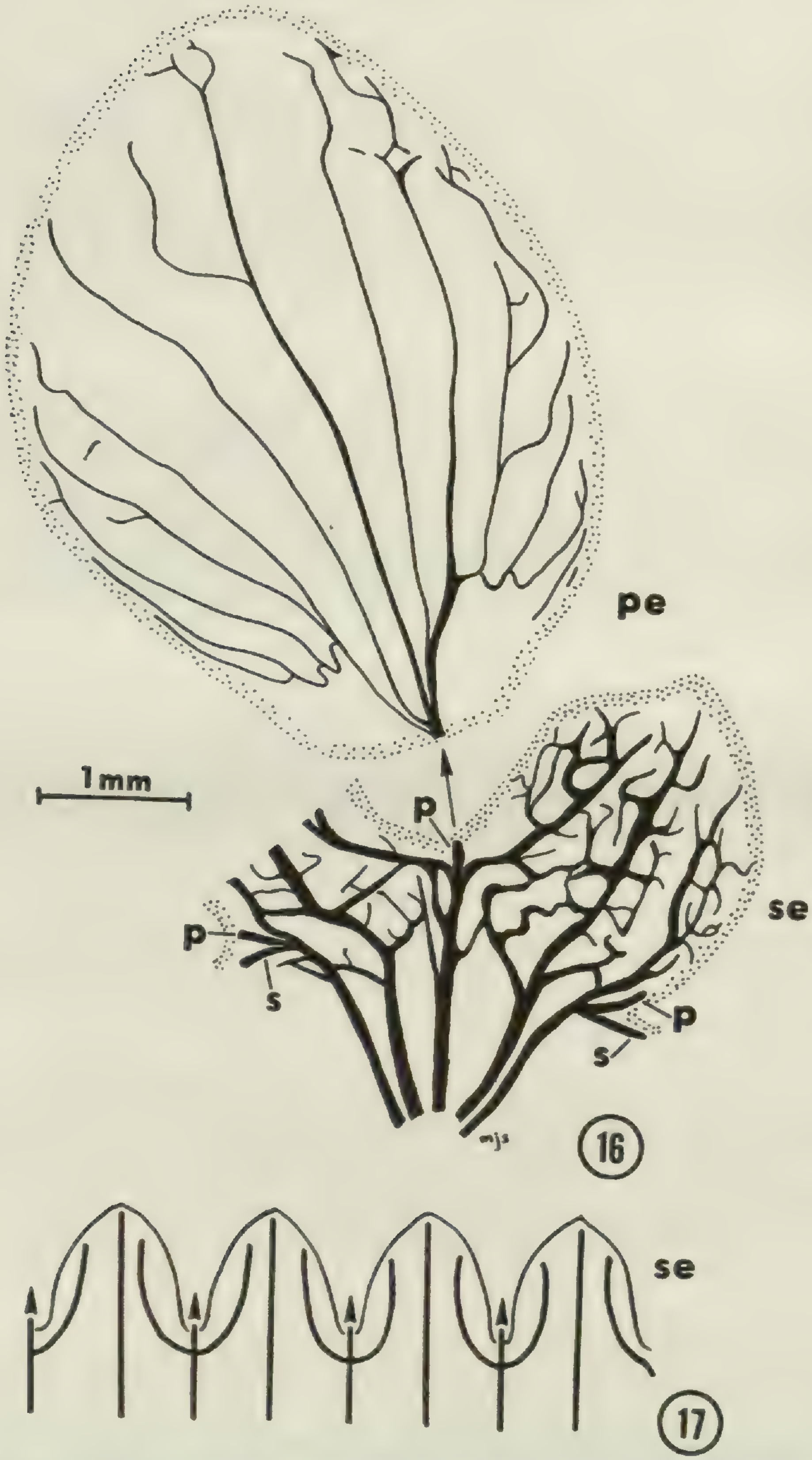
One collection of *E. biflora* "A" (*Hart 1048*) had been determined as var. *wallenii* (Macf.) Krug & Urban, and it is cited as such in Urban (1895). However, I am unable to see any clearcut anatomical differences between this variety and the other two collections of *E. biflora* "A" (*Pires & Westra 48813*; *Steyermark & Wurdack 31*).

In view of the anatomical differences between *Eugenia biflora* "A", "B", and "C", but in spite of the organographical similarities, this species apparently deserves taxonomic reappraisal.

HISTOLOGY. The dense silky or silky-strigose pubescence of simple hairs (see Schmid, 1972b, *Figure 12*, also like *Figure 9*) covering the floral tube and sepals is distinctive for this species (McVaugh, 1969).

VASCULATURE. The following description, based primarily on *Pires & Westra 48813*, pertains mainly to *Eugenia biflora* "A" and "B". For variations see above discussion and also TABLE II.

A single trace (several in *Steyermark & Wurdack 31*) supplies each bracteole. The vasculature of the floral tube and style is like that of *Eu-*



FIGURES 16, 17. **Eugenia biflora** (*Pires & Westra 48813*, MICH). FIGURE 16, Reconstruction of vasculature to and in three perianth parts; vasculature is complete. Only major vasculature indicated for most of floral tube. Vasculature to stamens and ovary omitted. FIGURE 17, Diagrammatic representation of major vasculature to perianth parts. Arrows indicate insertion of petals. ABBREVIATIONS: p, petal bundle; pe, petal; s, sepal bundle; se, sepal.

genia confusa (see TABLE II). However, as in several other species of *Eugenia s. s.* (e.g., *E. florida*, *E. oerstediana*, *E. uniflora*), in *E. biflora* there is a very regular relationship between the major bundles of the floral tube and the vasculature of the perianth parts (FIGURE 17). Eight major bundles, four sepal bundles alternating with four petal bundles, occur throughout the floral tube and produce many small minor, anastomosing strands (FIGURE 16). Distally, the four sepal bundles continue up the middle of the four sepals (FIGURES 16, 17). In contrast, each of the four petal bundles trichotomizes (FIGURES 16, 17), one of the three bundles that results entering each petal, the other two (lateral) bundles functioning as laterals of the two adjacent sepals. The bundle entering each petal branches profusely (FIGURE 16). The medial and two lateral bundles in each sepal anastomose extensively (FIGURE 16). A variable number of smaller bundles also enter the sepals (FIGURE 16).

The ovarian vasculature is of the FLORIDA-type (FIGURE 15), but exhibits considerable variability, even in the same plant. The lateral carpellary system, which is not very extensive, fuses with the dorsal bundles near the tops of the loculi. Two massive placental strands descend from points just above the loculi and terminate at a single placental plexus perforated by much parenchyma. The placental strands originate in a variety of ways, in some flowers mainly or exclusively from the two dorsal carpellary bundles. In addition slender placental strands frequently enter from the sides of the septum.

The dorsal bundles, which do not branch, originate at various levels, usually in the locular region, but often even near the base of the flower.

Eugenia coffeifolia DC.

See McVaugh (1969) and Urban (1895) for synonymy. Data were compiled mostly from the plant from St. Lucia since my preparations of the other collection were of poor quality. As far as I could tell, however, the two collections are very similar.

ORGANOGRAPHY and HISTOLOGY. The presence of only two ovules per locule is unusual in *Eugenia s. l.* (McVaugh, 1969), although as few as two or three ovules per locule also do occur in *E. oerstediana* (McVaugh, 1963a, b). The floral tube is strigose, with hairs similar to those in *Figure 7* in Schmid (1972b). The style is sparingly pilose.

VASCULATURE: See TABLE II. The ovarian vasculature is of the FLORIDA-type (FIGURE 15). Near the tops of the loculi a variable number of strands of the anastomosing lateral carpellary bundles, often along with strands derived from the dorsal carpellary bundles, fuse into two large placental strands, which terminate at a single placental plexus containing little or no interfascicular parenchyma. Occasionally, additional, slender placental strands enter the septum via its sides and fuse with the placental plexus. The vasculature of the other floral parts resembles that of *Eugenia capuli* (see TABLE II).

Eugenia salamensis Donn. Sm.

Synonyms include *Psidium rensonianum* Standl., *Eugenia mexiae* Standl., and *E. hiraeifolia* Standl. (see McVaugh, 1963a, b). I examined material of var. *salamensis* (this labelled *E. mexiae*) and var. *hiraeifolia* (Standl.) McV. Unless otherwise noted, the following comments apply to both varieties.

Although both varieties are "readily distinguished" on the basis of vegetative characters in particular, McVaugh (1963a, p. 457) considered them "surely conspecific." Although it is a matter of taxonomic opinion, there seem sufficient anatomical differences between the two varieties, as noted below, that both could deservedly be retained as separate species, particularly if such very (and even more) similar taxa as *Eugenia capuli* and *E. venezuelensis* (see TABLE II) are regarded as distinct.

ORGANOGRAPHY and HISTOLOGY. Dibrachiate trichomes (see Schmid, 1972b, *Figure 13*) with short to long, equal or unequal, often contorted arms are very abundant on the floral tube and sepals. Variety *hiraeifolia* was very tanniferous, var. *salamensis* only slightly so. The floral tube of the former is much more prolonged above the ovary than that of the latter (ca. 1.1 mm. maximum versus 0.2 mm. maximum, respectively). The only floral difference that McVaugh (1963a) noted for the two varieties was the slightly longer styles of var. *salamensis*. In buds, styles of var. *salamensis* are therefore doubled back whereas those of var. *hiraeifolia* are erect or nearly so.

VASCULATURE. See TABLE II. The ovarian vasculature of var. *salamensis* was studied in much more detail, but that of var. *hiraeifolia* seemed similar. The ovarian vasculature is of the FLORIDA-type (FIGURE 15). An anastomosing lateral carpellary system produces, usually just above the tops of the loculi, two massive placental strands that descend to the placental region. In addition, several slender placental strands frequently enter the sides of the septum.

The vasculature of the floral tube and style of var. *hiraeifolia* is, respectively, like that of *Eugenia florida* and *E. venezuelensis* whereas that of var. *salamensis* is like that *of E. confusa* (see TABLE II). Differences in vasculature between the two varieties include characters 8, 10, 18, and 20 in TABLE II. Variety *hiraeifolia* is much more heavily vascularized than var. *salamensis* and has many small anastomosing strands distributed between the loculi and the vascular cylinder of the floral tube.

Eugenia flavescens DC.

See McVaugh (1969) for synonymy.

HISTOLOGY. This is the only American species of *Eugenia s. l.* I studied that lacked secretory cavities in the anthers.

VASCULATURE. See TABLE II. The ovarian vasculature exemplifies the FLAVESCENS-type (FIGURE 18). An extensive lateral carpellary system consisting of slender anastomosing bundles girdles the loculi. From few

to many (up to about 11 per flower) placental strands depart from this lateral carpellary system, enter the septum, where they frequently anastomose, and terminate at the placental plexus (FIGURE 18). The dorsal carpellary bundles are connected to the lateral carpellary system at a number of points. Other features of floral vasculature resemble those of *Eugenia confusa* (see TABLE II).

Eugenia cartagensis Berg

HISTOLOGY. Phloem fibers occur throughout the pedicel, sclereids chiefly distally.

VASCULATURE. See TABLE II. The ovarian vasculature is of the FLAVESCENS-type (FIGURE 18). There are usually few placental strands, and in the septum these often fuse for a considerable extent. Bundles of the lateral carpellary system, which is not very extensive, anastomose chiefly near the tops of the loculi. The lateral and dorsal carpellary bundles are interconnected only at the tops of the loculi. Other features of floral vasculature are very much like those of *Eugenia confusa* or *E. flavescens* (see TABLE II) except that ten major bundles occur in some flowers of *E. cartagensis*.

Eugenia winzerlingii Standl.

One collection (*Lundell 851*) was analyzed most thoroughly. The three collections examined, however, are anatomically similar.

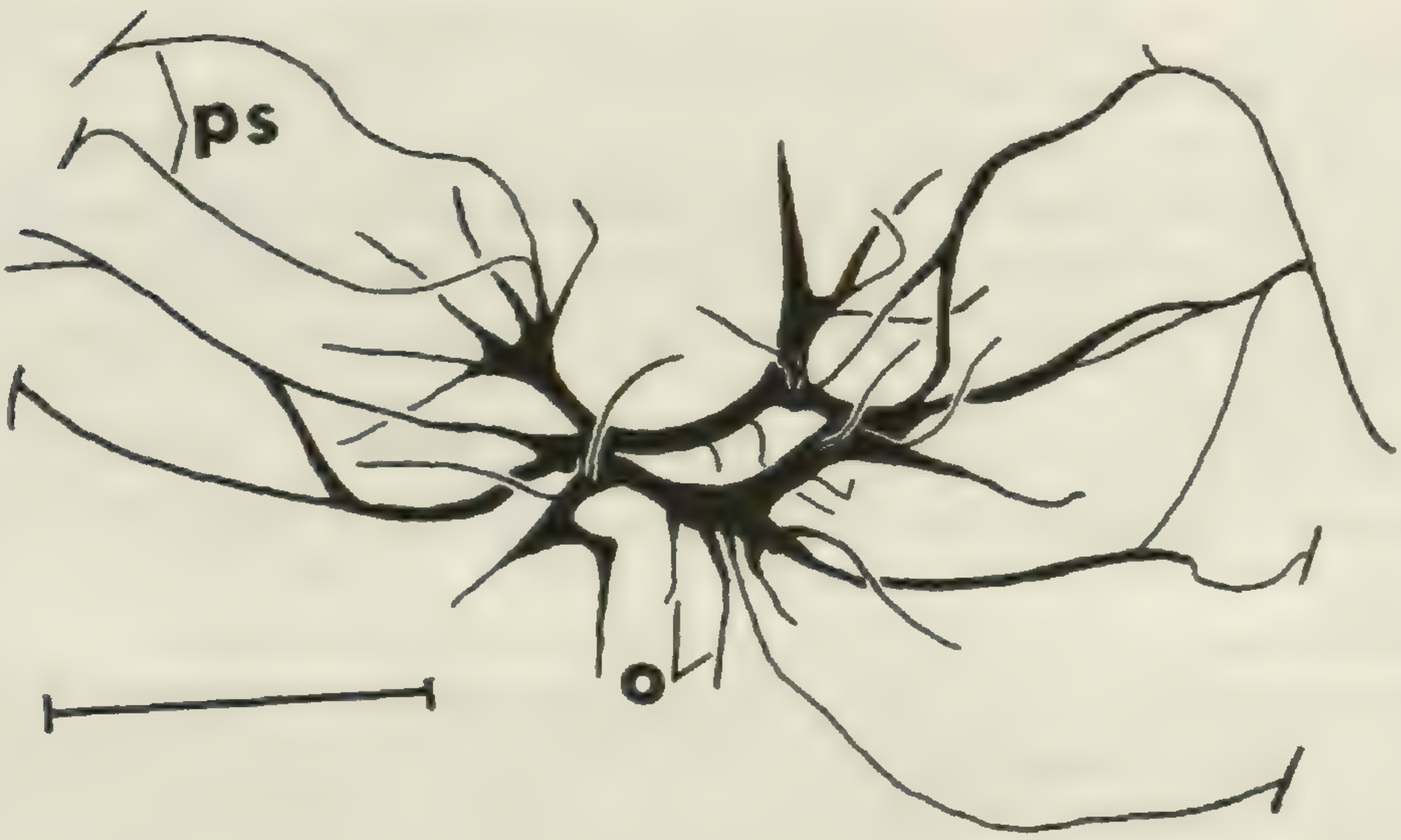
ORGANOGRAPHY and HISTOLOGY. The flowers are borne on filiform pedicels up to 20 mm. long (McVaugh, 1963b). The pedicels contain numerous narrow thin-walled phloem fibers commonly .4 to .5 mm. and often up to about .8 mm. long. One of the 14 flowers examined was tricarpellate; its placental vasculature was similar to that of the other flowers. Unlike other species I studied, the walls of the loculi of *Eugenia winzerlingii* are lobate.

VASCULATURE. See TABLE II. The ovarian vasculature is of the FLAVESCENS-type (FIGURE 18.) However, the following differences from *Eugenia flavescens* were noted: The lateral carpellary system is less extensive. Two separate placental strands, as in *E. confusa* (FIGURES 1, 3), are present. Placental strands occasionally originate directly from the dorsal carpellary bundles.

The vasculature of the floral tube and style resemble, respectively, that of *Eugenia confusa* (or *E. flavescens*) and *E. florida* (see TABLE II). A continuous ring of vascular tissue frequently occurs at the tip of the style.

Eugenia uniflora L.

Synonyms include *Myrtus braziliana* L., *Plinia rubra* L., *P. peduncula-ta* L. f., *Eugenia michelii* Lam., *Stenocalyx michelii* (Lam.) Berg, and *Eugenia decidua* Merr. [also "Myrtus indica" Tilli (1723); "Eugenia indica" Mich. (1729)] (see Berg, 1855–56; McVaugh, 1963b, 1969; Merrill, 1950; Urban, 1895). The two collections studied are similar.



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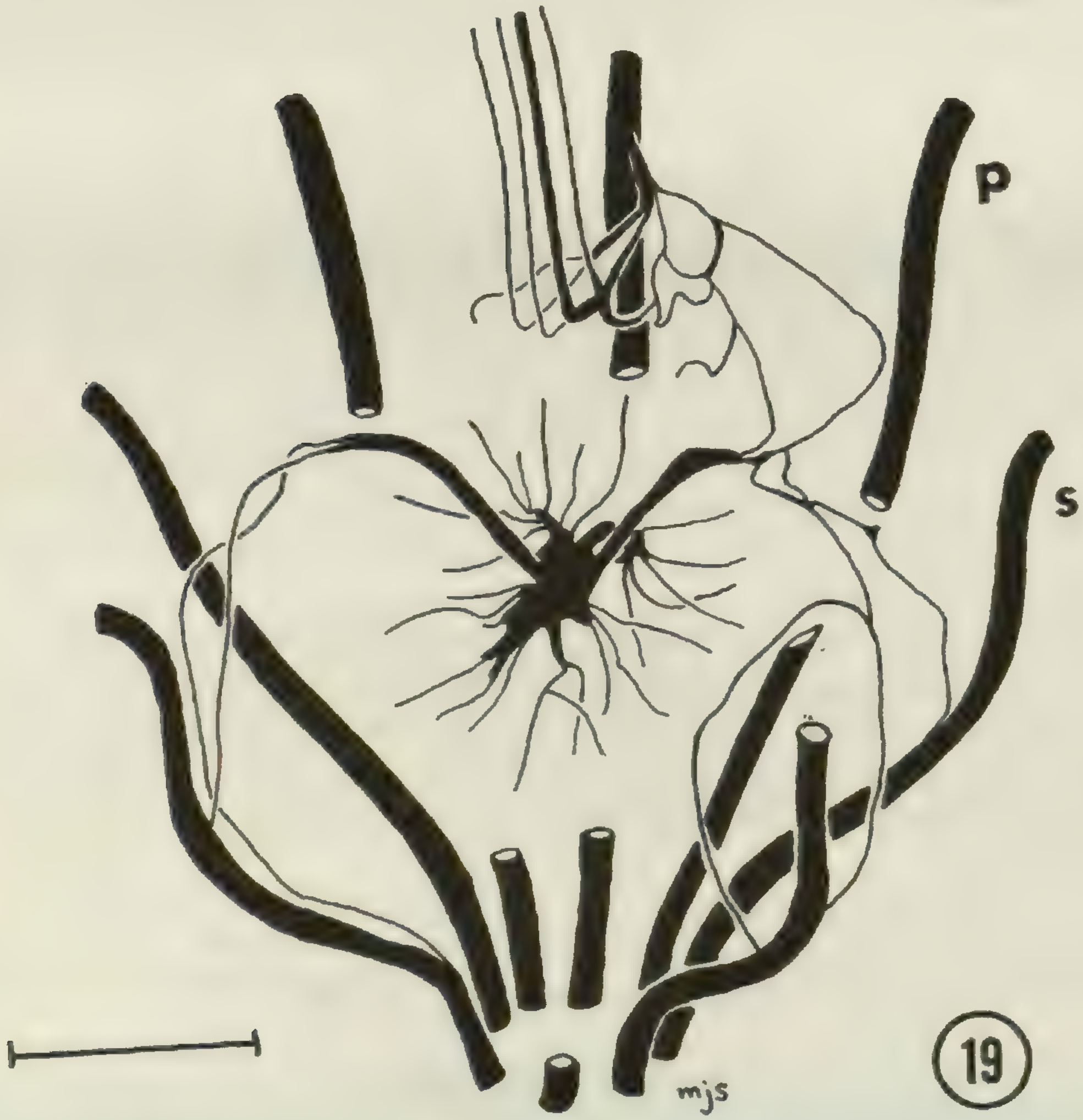

19

FIGURES 18 and 19. FIGURE 18, **Eugenia flavescens.** Reconstruction of placental system showing placental strands traversing septum and terminating at a placental plexus. FIGURE 19, **Eugenia uniflora** (*Taylor 48–1048*, MICH). Reconstruction of cleared flower showing eight major bundles of floral tube, placental vasculature, and half of the carpellary vasculature destined for style.

Eugenia uniflora L., the type of *Eugenia* Linnaeus (1753),[1] is a cultigen commonly known as pitanga, Brazil cherry, Cayenne cherry, Florida cherry, or Surinam cherry. This species is one of the very few native American species of *Eugenia s. l.* to have been studied anatomically (see Petit, 1908, for the histology of seed and fruit).

ORGANOGRAPHY and HISTOLOGY. The filiform pedicels (up to 18 mm. long, McVaugh, 1963b) contain long narrow phloem fibers, as in *Eugenia winzerlingii*. Most flowers of *E. uniflora* are entirely glabrous, but one collection (*Proctor 19469*) I examined has a hairy staminal disc (with hairs as in Schmid, 1972b, *Figure 6*, excluding the hair on extreme left of figure).

The floral tube is conspicuously eight-angled, with a large (up to 70 μ in radial dimension) major bundle opposite each rib. The loculi are very large in relation to the rather narrow walls of the inferior ovary. *Eugenia pleurocarpa*, with a slightly eight-angled floral tube, is the only other species of *Eugenia s. l.* (31 studied in all, Schmid, 1971, 1972a–c) to have either of these characters. The fruit of *E. uniflora* is also prominently eight-costate.

VASCULATURE. See TABLE II. The vasculature of the floral tube is similar to that of *Eugenia biflora* (see TABLE II, FIGURES 16, 17). However, other features of vasculature of *E. uniflora* are quite distinctive, particularly the ovarian vasculature, which exemplifies the UNIFLORA-type (FIGURE 19). Several placental strands originate from various sources and at various levels in the floral tube (FIGURE 19), much as in *E. confusa* (FIGURE 1). On entering the septum, the placental strands usually fuse into two large compound placental strands. These turn downward as they traverse the septum and then terminate at a single placental plexus usually consisting of a solid mass of vascular tissue (FIGURE 19).

Unlike the species of *Eugenia s. s.* previously described, discrete dorsal carpellary bundles are not readily definable. Usually two large bundles originate in the positions where the dorsals would ordinarily be expected. These bundles, however, each quickly split into several fine, anastomosing strands (FIGURE 19), most of which eventually continue into the style. Occasionally, other carpellary bundles also supply the style. There are frequent connections between the placental vasculature and the strands supplying the style (FIGURE 19). The many stylar bundles (as many as 12 in the base of the style) occasionally branch and often form a continuous ring of vascular tissue at the stylar apex. A comparable situation occurs in certain species of *Alangium* (Eyde, 1968), but here, in contrast to *E. uniflora*, the two groups of fine, anastomosing strands taking the

[1] Authorities and dates of publication of genera follow the *Index Nominum Genericorum*, which should be consulted for details.

Other vasculature of floral tube and ovary and outlines of ovarian loculi omitted. Four sepal bundles alternate with four petal bundles. ABBREVIATIONS: o, ovular trace; p, petal bundle; ps, placental strand; s, sepal bundle. Magnification bars equal 250 μ.

place of the dorsals each fuse, forming a pair of well defined bundles that traverse the style.

OTHER TAXA WITH TRANSEPTAL OVULAR SYSTEMS

All the species of *Eugenia s. s.* listed below have transeptal ovular systems. In addition, all taxa have closed vascular systems, with the usually eight major bundles of the floral tube exhibiting a monocyclic arrangement. Vascular tissue extends to the apex of the style. The flowers lack sclerenchyma. However, the precise nature of these and other characters was not determined for these species for several reasons, in part because my clearings and many of my sections were of poor quality, and also because most of the buds of these species are very large and have extensive vascular tissue. A few distinctive features, chiefly of pubescence, are noted below.

(1) *Eugenia acapulcensis* Steud. See McVaugh (1963a, b) for synonymy. My material is glabrous, except for a slightly hairy staminal disc (with hairs like those in Schmid, 1972b, *Figure 5*).

(2) *Eugenia aeruginea* DC. Synonyms include *E. fadyenii* Krug & Urban ex Urban (see McVaugh, 1963b). The floral tube and sepals have an appressed, dense pubescence of dibrachiate hairs (as in Schmid, 1972b, *Figure 11*).

(3) *Eugenia duchassaingiana* Berg. The sepals and floral tube are very pubescent, with hairs as in *Figure 7* in Schmid (1972b).

(4) *Eugenia gregii* (Sw.) Poir. Synonyms include *Myrtus gregii* Sw., *Greggia aromatica* Solander ex Gaertn., and *Eugenia sieberiana* DC. (see Urban, 1895). *Eugenia gregii* is the type of the segregate genus *Greggia* Solander ex J. Gaertner (1788). This species has very distinctive infundibuliform hairs (see Schmid, 1972b, *Figure 8*) that form a dense mat on the floral tube and abaxial surfaces of the perianth parts. Other than these unusual hairs, however, the species certainly does not have any feature that might justify acceptance of the segregate genus *Greggia*. Superficially, the ovarian vasculature is of the FLORIDA-type (FIGURE 15).

(5) *Eugenia mandevillensis* Urban. Only the staminal disc and style are hairy (see Schmid, 1972b, *Figure 9*).

The secretory cavities are so remarkable in their (a) size, (b) abundance, and (c) distribution that this species might well be called the "American clove" of *Eugenia s. s.* (a) Size: The secretory cavities are, on the average, larger than those of any other species of *Eugenia s. l.* I have seen, including those of clove (*Syzygium aromaticum*, see Schmid, 1972b, c). At about 350 microns in dimension, the largest cavities are comparable in size to the largest of *S. aromaticum* and *S. malaccense*. (b) Abundance: The secretory cavities of *E. mandevillensis* are more numerous than those of any other species of *Eugenia s. l.*, with the possible exception of clove. In many parts of the flower, which is about 8–

9 mm. long in bud, the secretory cavities are so numerous that they occur as chains separated only by a few layers of epithelial cells. (c) Distribution: As in clove, the secretory cavities in the floral tube and the top of the ovary of *E. mandevillensis* frequently occur in two and even three intermixed layers (compare with *Figures 48, 49, 55, 56,* in Schmid, 1972c). Many cavities occur in the anthers (up to about seven per anther), filaments, and style, again as in clove. Unlike those of any other species of *Eugenia s. l.*, however, the secretory cavities of *E. mandevillensis* also occur in the ovarian tissue adjacent to the loculi and below them.

(6) *Eugenia muricata* DC. See McVaugh (1969) for synonymy. Many appressed-ascending, silky hairs (see Schmid, 1972b, *Figure 7*, also as in *Figure 12*) cover the floral tube and sepals.

(7) *Eugenia pleurocarpa* Standl. The floral tube and sepals are tomentose, covered by a pubescence of dibrachiate to mostly simple hairs of variable morphology (see Schmid, 1972b, *Figures 10, 11*). The flowers are very tanniferous, much more so than any other species of *Eugenia s. s.* I studied. See also remarks under *Eugenia uniflora* above.

(8) *Jossinia aherniana* (C. B. Rob.) Merr. Synonyms include *Eugenia aherniana* C. B. Rob. and *E. melastomoides* Elm. (see Merrill, 1950). The simple to dibrachiate hairs are figured in Schmid (1972b, *Figure 6*).

For vasculature see TABLE II. The floral vasculature is similar to that of the species of *Eugenia s. s.* described above except, that the flowers of *Jossinia aherniana* seem much more heavily vascularized. The placental vasculature of this species, however, is supplied not only transeptally by strands from the periphery of the septum, as in the previously described species of *Eugenia s. s.*, but also by a few bundles entering from the base of the septum, somewhat as in *Syzygium s. l.* (see Schmid, 1972c). In sharp contrast to *Syzygium s. l.*, however, the characteristically massive axile strand is lacking. In all, the ovarian vasculature most closely resembles the FLAVESCENS-type (FIGURE 18).

(9–10) Only fruiting material of the following two species, both from the Old World, was available. Both taxa have closed vascular systems and about eight major bundles of the floral tube in a monocyclic arrangement. Considerable vascular tissue occurs in the floral tube. The staminal discs of both species are hairy, more or less as in *Figures 6* and *9* in Schmid (1972b). Sclerenchyma occurs only in the seeds of *Jossinia palumbis* but throughout the fruit of *Eugenia whytei*, which has both fibers and sclereids. The vascular supply to the ovules seems to be of the transeptal type, but this conclusion is based on the examination of large, mature, one-seeded fruits in which there had been considerable displacement and disruption of the septum.

(9) *Eugenia whytei* Sprague in Stapf. Chattaway (1959) conjectured that this might represent a species of *Jossinia* rather than *Eugenia*.

(10) *Jossinia palumbis* (Merr.) Diels. Synonyms include *Eugenia palumbis* Merr. (see Diels, 1921).

DISCUSSION AND CONCLUSIONS

The transeptal ovular supply, which was found in all 23 species studied, varies considerably in structure even between different flowers of the same plant. As discussed in Schmid (1972b), the nature of the vascular supply to the ovules — transeptal in the mainly New World genus *Eugenia s. s.* versus axile in the exclusively Old World genus *Syzygium s. l.* — is the most distinctive anatomical difference between these taxa. In addition, other evidence from both reproductive and vegetative anatomy and morphology also supports the fundamental disparity of these two taxa (Schmid, 1971, 1972b). While there seems to be convincing evidence that most Old World species of *Eugenia s. l.* are distinct from the New World ones (Schmid, 1971, 1972b), it is more difficult to differentiate, anatomically, between the various segregate genera of *Eugenia s. s.*[2]

Except for the taxa discussed below, most of the species of *Eugenia s. s.* I analyzed have never been placed in segregate genera. Consequently, my conclusions on the various species relationships seem more appropriately discussed above where the species are first described.

Eugenia gregii is the type species of the segregate genus *Greggia* Solander ex J. Gaertner (1788). However, only the authors who proposed it seem to have accepted this segregate. The floral anatomy of *E. gregii* is entirely consistent with its placement in *Eugenia s. s.*

Stenocalyx Berg (1856), characterized by precocious flowers, has also won little credibility among botanists. Bentham (1869) condemned the use of so vague and variable a feature, and nearly a hundred years later McVaugh (1968) concurred. However, Kausel (1957, 1966), the arch splitter of the Myrtaceae, still assesses *Stenocalyx* as valid. Anatomically, *Eugenia uniflora* (= *Stenocalyx michelii*), the type species of *Stenocalyx* (as well as of *Eugenia* Linnaeus, 1753), is certainly at home in *Eugenia s. s.* To be fair, however, this species is undeniably different in many respects from most other species of *Eugenia s. s.* (see TABLE II). In addition, Chattaway (1959) found *E. uniflora* to differ from the majority of the New World species in its bark structure. These differences, however, merely reinforce the notion that *E. uniflora* and its relatives occupy a somewhat isolated position within the genus. The anatomical differences do not justify generic status, however, since they merely conform to the great anatomical (and organographical) diversity of a very kaleidoscopic genus (see Schmid, 1972b). Actually, in view of the variation that *Eugenia s. s.* exhibits, I am not at all certain that *E. uniflora* and its relatives

[2] See McVaugh (1968) for an excellent discussion of the taxonomy of the American Myrtaceae, and also Kausel (1957), McVaugh (1968), and Niedenzu (1893) for generic synonymy of *Eugenia s. s.*

are even worthy of subgeneric rank, the status to which Niedenzu assigned them (1893) in his taxon *Macrocalyx*. Indeed, Bentham (1869) long before pointed out the great polymorphy of calyx structure in *Eugenia*, which became the basis for Niedenzu's characterization.

The floral anatomy of the Old World genus *Jossinia* Commerson ex De Candolle (1828) is very similar to that of the American species of *Eugenia s. s.* (see TABLE II), differing only in the nature of the vascular supply to the ovules. All the evidence from both vegetative and reproductive organography and anatomy now available (see Schmid, 1971) demonstrates that *Jossinia* is so very similar to the American species of *Eugenia s. s.* that segregation of *Jossinia* as a genus seems unwarranted. *Jossinia* may well represent a residue of Old World species of *Eugenia s. s.* that, in some of its taxa, exhibits a rather primitive transeptal ovular system, one perhaps transitional between the axile ovular system of the Old World *Syzygium s. l.* and the transeptal ovular system of the New World species of *Eugenia s. s.* (Schmid, 1971). These aspects will be elaborated in a subsequent publication in this series (Schmid, in preparation).

SUMMARY

There seems to be no anatomical basis for the recognition of the following generic segregates of *Eugenia s. s.*: *Greggia*, *Jossinia*, and *Stenocalyx*. *Stenocalyx* admittedly occupies a somewhat isolated position within *Eugenia s. s.*, but the differences of the former merely conform to the great organographical and anatomical diversity of a very kaleidoscopic genus. The organography and anatomy of the Old World *Jossinia* species are very similar to those of the American species of *Eugenia s. s.*

The following conclusions were drawn about the relationships of various species of *Eugenia s. s.* (1) *Eugenia capuli*, *E. tikalana*, and *E. venezuelensis* represent a complex of very closely related species. (2) *Eugenia florida* is best regarded as a widely distributed complex comprised of such scarcely distinguishable forms or varieties as *E. oerstediana*, *E. conzattii*, and *E. cocquericotensis*. (3) *Eugenia salamensis* varieties *salamensis* and *hiraeifolia* seem sufficiently distinct so that at least varietal and probably specific status is justified. (4) *Eugenia biflora* was found to contain a number of anatomically different but organographically similar forms and deserves taxonomic reappraisal.

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VENATION PATTERNS IN THE LEAVES OF EPHEDRA

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THE VIEW IS WIDELY HELD that the vascular supply of the leaf in *Ephedra* consists of two traces associated with a unilacunar type of node (Marsden & Steeves 1955). This interpretation has brought *Ephedra* prominently into recent discussions of the phylogenetic status of the unilacunar, two-trace type of vasculature which occurs not only in *Ephedra* and certain other gymnosperms but which is also characteristic of the cotyledonary and foliage-leaf nodes of a number of dicotyledons (Marsden & Bailey 1955; Bailey 1956).

The considerable attention which has been devoted to the nodal anatomy of *Ephedra* has not been accompanied by comparably detailed studies on the foliar venation in any of the numerous species of this genus. This overt neglect of venation probably is due in large part to the fact that the very small "reduced" leaves, apparently characteristic of the majority of species, have not seemed very promising types of appendages for detailed comparative studies. My survey of the voluminous literature on *Ephedra* failed to reveal a single drawing or photomicrograph illustrating the venation pattern as it would appear in cleared, stained foliage leaves. As far as I could discover, the great majority of previous descriptions of leaf venation in *Ephedra* were based on reconstructions derived from a study of serial transections of buds or mature nodes. One of the few exceptions which I have encountered occurs in the recent paper by Lehmann-Baerts (1967) who made considerable use of cleared and stained whole mounts in her study of "tracheogenesis" in the paired veins of developing cotyledons and primary leaves of several species of *Ephedra*. It is also evident that Scheit (1883) employed clearing techniques in his study of venation and transfusion tissue in the leaves of *Ephedra altissima* and *Gnetum gnemon*.

On the basis of the information provided by serial transections, the great majority of investigators reached the conclusion that the venation of an *Ephedra* leaf consists of a pair of veins which neither branch nor anastomose during their course through the sheath and lamina (Marsden & Steeves 1955, p. 244; Napp Zinn 1966, pp. 173–174). The largely neglected investigations of Monoyer (1937; 1938, a, b, c) however, revealed for the first time that the leaf trace in certain species of *Ephedra* may be trifasciculate. In most of the species he studied, only the two lateral members of the trifasciculate trace extend into the leaf while the median trace ends at the nodal girdle as the result of an arrest in its upward development, a process which Monoyer (1938, b, c) termed "acrolysis." But in *E. fragilis* var. *campylopoda*, Monoyer (1937) found that *each* member of a leaf pair consistently has three veins, a median

"M" and two lateral veins, "L,L." This unusual type of venation is illustrated in his paper by drawings of transections at two different levels through a bud (see Monoyer 1937, *plate II, Figs. 1, 2*). Monoyer's studies led him to conclude that the three-veined type of vasculature may represent the "primitive" condition in *Ephedra* and that the more common two-veined condition is derivative.

The occurrence of three-trace leaves, as reported by Monoyer, raises important but as yet unsolved questions concerning nodal evolution and venation in the genus as a whole. In their survey of nodal anatomy in nine species of *Ephedra*, Marsden & Steeves (1955, *Text-figs. 3–5*) described and illustrated, for both decussate and whorled phyllotaxies, the presence of internodal "complementary bundles" comparable in position to Monoyer's median leaf traces. Marsden & Steeves also noted that the complementary bundles usually extend from one nodal girdle to the next "without in any way joining the leaf traces." In rare instances (e.g. *E. altissima*) however, they found that "the complementary bundle extends into the leaf as a third trace."

In the light of the conflicting interpretations of leaf venation in *Ephedra*, I decided to explore as thoroughly as possible, the venation patterns of a species in which complementary bundles and three-veined leaves occur. A preliminary examination of available cultivated material indicated that *E. chilensis* Miers would be suitable for study, especially since the nodal and internodal anatomy of this taxon had already been analysed in detail by Marsden & Steeves (1955, *Text-fig. 5*). The other two species included in the present study, *E. foliata* Boiss. and *E. altissima* Desf., were chosen because in both the leaf fluctuates greatly in size, in some cases reaching a length of 1.5 to 2 cm. The conspicuous variation in leaf dimensions allows one to compare the venation patterns of scale-like leaves with those of the well-developed needle-like leaves.

MATERIALS AND METHODS

Material of the three species of *Ephedra* included in my study was obtained from the following sources: *E. foliata* (1) shoots from plants growing in the University of California Botanical Garden at Berkeley and in the Botanical Garden, University of Delhi, India, and (2) specimens from the herbarium of the University of California, Berkeley (*Barkley 32 Ir 2299*; *Stewart 14663A*); *E. altissima*, shoots from plant No. 79214 growing at the Plant Introduction Station, Chico, California; *E. chilensis*, cultivated plant No. 49542 in University of California Botanical Garden (voucher specimens deposited in U. C. Herbarium). It is a great pleasure to express my thanks to Dr. B. M. Johri for the preserved material of *E. foliata* and to Dr. R. L. Smith for the living specimens of *E. altissima*.

Individual leaves, removed from the nodes by tangential longitudinal cuts, as well as nodal segments with attached leaves, were cleared by prolonged treatment in 5–10% NaOH followed, after thorough washing in water, by chloral hydrate. The leaves and nodal sectors of living ma-

terial which had been fixed in 50% alcohol or formalin-acetic acid-alcohol were more refractory than herbarium specimens and it was necessary to accelerate the clearing phase in NaOH by placing the specimens in petri dishes on an electric slide-warmer for long periods of time.

Very instructive preparations of *E. chilensis*, showing the complete venation of each member of a leaf-pair and the basal connections of the respective leaf traces were secured by making careful longitudinal cuts between the leaves and through the node and subjacent internode of cleared segments of the shoot. The separated halves were then dehydrated in the usual alcohol series and stained for several hours in a 1% solution of safranin in equal parts of absolute alcohol-xylene. After destaining in alcohol-xylene, the specimens were mounted in "Piccolyte." Similar procedures were followed in processing and staining detached leaves of all the species included in the present study.

Satisfactory photomicrographs of *E. chilensis* showing clearly the venation pattern and the mode of attachment of the leaf traces proved difficult to obtain by means of transmitted light because of the very numerous fibers adjacent to the veins in the leaf sheath region. The problem was solved by Mr. A. A. Blaker who employed a combination of directional dark field and transmitted light in which the dark field is oriented along the longitudinal axis of the specimen. Under these lighting conditions, the veins, leaf traces, and internodal vascular strands appear brilliantly refractive and distinct from the fibers and other tissues (see PLATES IV, V). I wish to thank Mr. Blaker for his skillful preparation of these illustrations as well as for the other photomicrographs used in this paper.

LEAF MORPHOLOGY

In the genus *Ephedra* which comprises about 35 described species (Markgraf 1926), the leaves occur in pairs or whorls at each node and are basally connate, forming a more or less conspicuous sheath. Napp-Zinn (1966, p. 173) uses the term "gamophyll" to designate the fused character of the leaves. Although the classical monographs of Meyer (1849) and Stapf (1889) plainly reveal the considerable fluctuation in the size and proportion of the lamina in *Ephedra* leaves, this variability is either minimized or disregarded in many modern descriptions. A few typical examples of misleading generalizations will be given to illustrate this point. Pearson (1929, pp. 1, 2), in his well known monograph on the Gnetales, states that in *Ephedra* "the assimilating stems are slender and grooved and bear whorls of reduced leaves; they clearly resemble the aerial shoots of *Equisetum*." But he adds that in *E. altissima*, *E. foliata*, and *E. gracilis*, the leaf blade "is developed only at the middle and the upper nodes." Another vague description occurs in Chamberlain's (1935) text on the gymnosperms, in which it is stated that "the leaves are small and rudimentary, and, even when young, are of scarcely any importance in the vegetative economy of the plant." Zimmermann (1959,

p. 460) and Sporne (1965, p. 184), respectively, describe the foliage of *Ephedra* as "decussate scale-leaves" and as "reduced to minute scales."

In contrast to these characterizations, Stapf (1889) noted that although in the majority of species the leaves are reduced to sheaths, a well-developed lamina occurs in some leaves of *E. altissima*, *E. foliata*, *E. gracilis*, and *E. americana* var. *andina*, reaching in individual cases a length of 3 cm. and a width of 1 to 1.5 mm. In all these species, the lamina is delicate and ultimately abscisses from the persistent sheath. It seems likely that the persistent sheathing bases of the leaves of herbarium specimens may often be mistaken for *complete* "scale-leaves."

It will now be appropriate to describe briefly the results of the present investigation on leaf morphology. A well-developed leaf in both *E. foliata* and *E. altissima* consists of a basal sheath, joined by a membranous commissure with the other leaf or leaves at the node, and a subulate lamina (TEXT-FIG. 3; PLATE I: 1, 3, 4). The total length (i.e. sheath + lamina) of leaves of this type varies considerably; small leaves, with weakly-developed laminae, measure only 8 to 9 mm. in length while the longest leaves studied are 1.5 to 2 cm. long. No examples of leaves 2.5 to 3 cm. long, as found by Stapf (1889) in *E. foliata*, were encountered in the present study. In both *E. altissima* and *E. foliata*, the foliar appendages of the basal nodes of the shoot tend to be relatively small, with laminae measuring only 3 to 4 mm. in length (TEXT-FIG. 4). There is obviously however, no sharp demarcation between "well-developed" and scale-like leaves. Very commonly a single shoot during its development may form a graded series of appendages, with the smaller leaves at the base and the longer, better developed leaves restricted to nodes in the middle region.

The *consistently* smaller laminae of the leaves of *E. chilensis* correspond to some of the current descriptions regarding the "reduced" nature of *Ephedra* leaves. In *E. chilensis* the phyllotaxis is variable in a single individual: well-developed shoots commonly — although not invariably — form three-leaved whorls whereas the leaf arrangement on the more slender lateral shoots is usually decussate. Regardless of phyllotaxis, the leaf consists of a prominent sheath and an extremely small lamina (TEXT-FIG. 5; PLATES IV–VI). In my material, the average length of the leaf is approximately 5 mm., a dimension which falls within the size range of 4.1 to 6.1 mm. noted by Miers (1869, pp. 164, 165) in his description of *E. chilensis*.

VENATION PATTERNS

Review of Literature. As I have indicated in the introduction of this paper, the consensus of opinion in the literature is that the venation of the leaves (including the cotyledons) of *Ephedra* consists of two unbranched veins which represent the upward extension of a pair of leaf traces (TEXT-FIG. 1). In a comprehensive survey of the old as well as the modern literature I have been struck by the vague and extremely brief descriptions of this venation pattern. It would be tedious to review

chronologically the various statements because of their repetitive character (see for example, the descriptions given by Thompson 1912, Goebel 1932, Troll 1938, Campbell 1940, Marsden & Steeves 1955, and Sporne 1965). It was particularly surprising to find that in Pearson's (1929) description of *Ephedra*, no mention is made of foliage-leaf venation. His account of vasculature in the adult shoot is strictly limited to nodal anatomy and the course of the double leaf traces in the eustele.

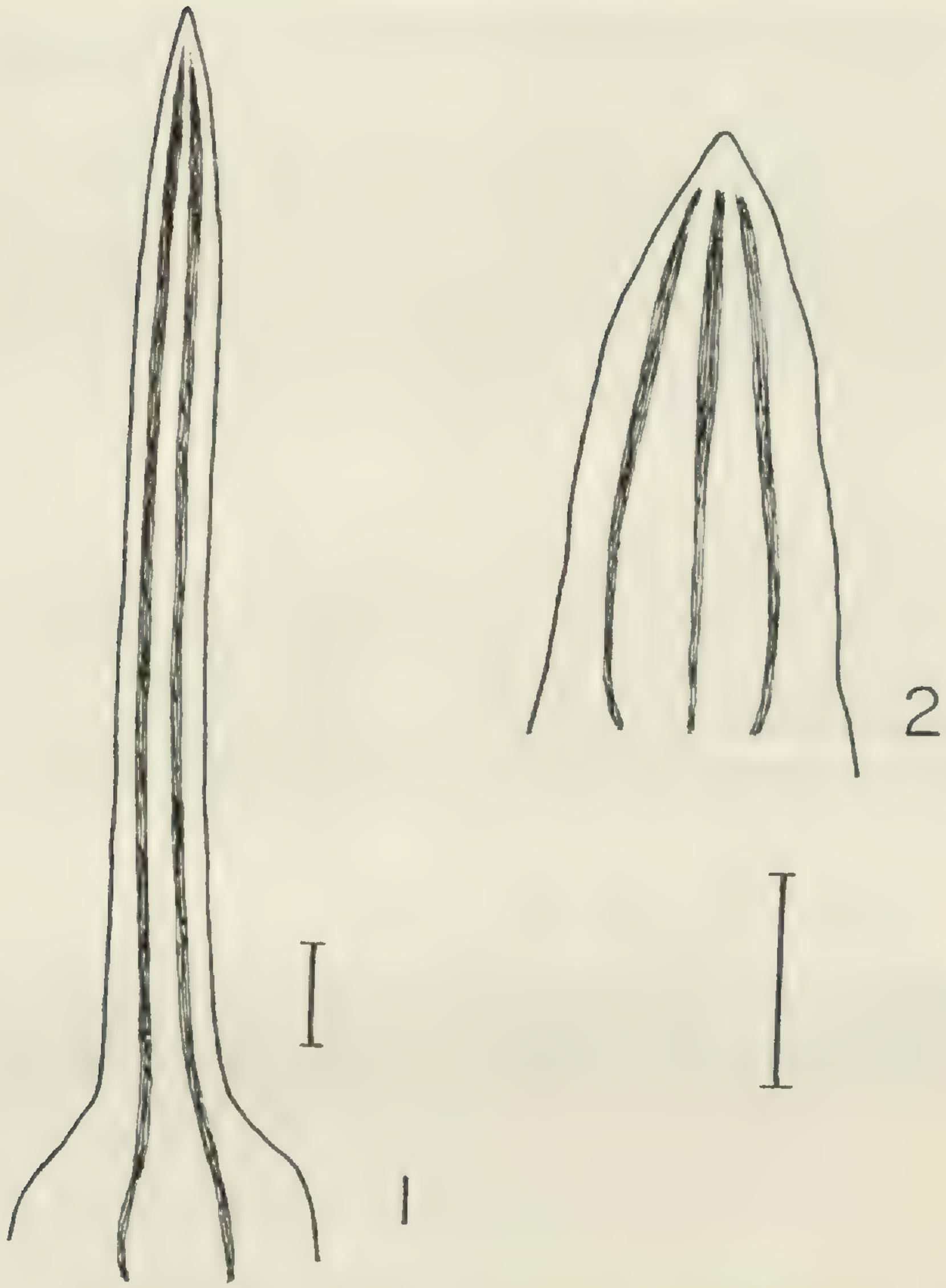
Many authors, who make a casual reference to venation, describe the venation of an *Ephedra* leaf as "parallel." Geyler (1867–68, p. 142) for example, in his classical paper on leaf-trace systems in gymnosperms, stated with reference to *E. equisetiformis* that the two bundles belonging to the leaf trace "extend together parallel and unbranched in the leaf." Similar descriptions of "parallel" venation in *Ephedra* were subsequently repeated by Bertrand (1874), Stapf (1889), Voth (1934), and Maheshwari & Vasil (1961). Eames (1952, p. 92) was particularly impressed by the course of the leaf veins in *Ephedra* and remarked: "The parallel-veined linear leaf resembles that of the cordaites and conifers in general type. It usually has two traces, typically widely separated in origin, though in some species there are said to be two traces arising side by side, or there may be only one trace. In the cordaites also the leaf has one or two traces."

As indicated previously, doubt as to whether the two-trace pattern of foliar vasculature is consistent throughout the genus *Ephedra* arose through the investigations of Monoyer (1937, 1938, a, b, c). His observation that the leaves of *E. fragilis* var. *campylopoda* are provided with an additional vein situated between the two lateral veins, raises important questions which I will discuss later in the paper. For purposes of general orientation, however, reference at this point should be made to TEXT-FIGURE 2 which illustrates the three-veined pattern which I have found in certain leaves of *E. chilensis*.

Venation Patterns in Ephedra foliata and E. altissima. The vasculature of the leaves of these species consists of two veins which either terminate freely near the leaf apex or are connected by transfusion tracheids at variable levels in the lamina (PLATES I and II). This fundamental similarity in venation patterns is interesting from a systematic viewpoint because Stapf (1889, p. 35) included both species in the "Tribus *Scandentes*" under the section PSEUDOBACCATAE. In his opinion, the "Tribus *Scandentes*" comprises "a very natural group" of species.

The comparative study of venation patterns in a relatively large number of cleared stained leaves emphasizes that the veins are not "parallel" in their course through the leaf, as has been repeatedly asserted in the general literature on *Ephedra*. On the contrary, the two veins, which may be either widely spaced or closely approximated in the leaf sheath, progressively *converge* towards the lamina-apex (PLATE I).

A salient feature of leaf anatomy in *Ephedra foliata* and *E. altissima* is the more or less profuse development of "transfusion tracheids." This term is used to designate the relatively short box-shaped cells, with reticu-



FIGURES 1, 2. Contrasted patterns of open leaf venation in *Ephedra*. FIGURE 1, two-veined leaf of *Ephedra foliata*. FIGURE 2, three-veined leaf of *E. chilensis*. The scale near each drawing equals 1 mm.

late or reticulate-pitted walls which occur along the borders of the xylem strands and which in many cases form a compact tissue between the vein tips (PLATE II: 5–7). As far as I am aware, Scheit (1883, p. 626) was the first to observe and describe the transfusion tracheids in the leaf of *E. altissima*. He introduced the term "tracheid-border" ("Tracheidensaüme") to designate the wing-like extensions of tracheids associated with the foliar veins of certain gymnosperms. In *E. altissima*, according to Scheit, reticulately thickened tracheids cover the vein endings as a cap-like mass of cells. The occurrence of transfusion tracheids in this species was also briefly noted by Thompson (1912, p. 1098). But since he relied on leaf transections rather than cleared leaves, he greatly underestimated the abundance of transfusion tracheids by stating that "at the edges of the bundle, as Strasburger has noted, there is an occasional transfusion tracheid which can be distinguished by its bordered pits and thickening bars."

The general venation pattern of the leaves of *E. foliata* and *E. altissima* may be described as either "open" or "anastomosed," depending on the degree of development of transfusion tracheids. If transfusion tracheids are restricted to the borders of the veins, the latter terminate freely at the lamina apex and the venation is "open." This condition has been observed in well-developed leaves measuring 1 to 1.5 cm. in length as well as in the more rudimentary laminae of scale-like leaves (TEXT-FIG. 1, 3, 4; PLATE I: 1, PLATE II: 5, 6). Anastomosed venation occurs when the adjacent borders of transfusion tracheids merge to form a wedge of tissue between the vein-tips (PLATE I: 2–4; PLATE II: 7). There is no sharp demarcation however, between open and anastomosed venation. A number of the leaves studied had definable vein-tips which were joined for only a very short distance by a few intervening transfusion tracheids (PLATE I: 4). Furthermore, it should be emphasized that great variation exists with reference to the level in the lamina at which the two veins first become confluent. In the leaves of cultivated plants of *E. foliata*, for example, the convergence of the two veins often begins well below the lamina-apex and, in extreme cases, the veins are confluent at such a low level that nearly half the lamina is vascularized by an apparently single massive strand of xylem and transfusion tracheids (PLATE II: 8).

Venation Patterns in Ephedra chilensis. The distinctive feature of the foliar vasculature of this species is the interpolation, in certain leaves, of a midvein between the two major lateral veins (PLATES IV, V). One of the most puzzling aspects of this type of venation is its sporadic and unpredictable occurrence among the leaves of a single node. TEXT-FIGURE 5 illustrates this point with reference to a three-leaved whorl: one leaf, B, is provided with three freely-terminating veins while each of the other two leaves is vascularized by a pair of veins as shown in A. Comparable variations seem to occur even more frequently in relation to decussate phyllotaxis. Most commonly, both members of a leaf-pair are two-veined but in some of the cleared nodal sectors, one leaf may possess a midvein while the other appendage conforms to the predominant two-veined pattern of vasculature (PLATE IV, A, B). Only a single example was found in which *both* members of a leaf-pair were three-veined.

In order to compare the nodal anatomy of two- and three-veined leaves in *E. chilensis*, selected nodal segments were split longitudinally and the two halves stained in safranin. Preparations of this type clearly reveal the independence between the complementary bundle and the traces which supply a two-veined leaf. As is shown in PLATE III, the complementary bundle terminates abruptly in a mass of transfusion tracheids at the node whereas the two leaf traces are attached to separate parts of the eustele. On this point, my observations fully agree with the reconstruction of nodal and internodal vasculature diagrammatically shown by Marsden & Steeves (1955. *Text-fig. 4*). The nature of the vascular connections of three veined leaves in *E. chilensis*, however, was not included in their description and illustrations of the nodal anatomy of this species. During the present

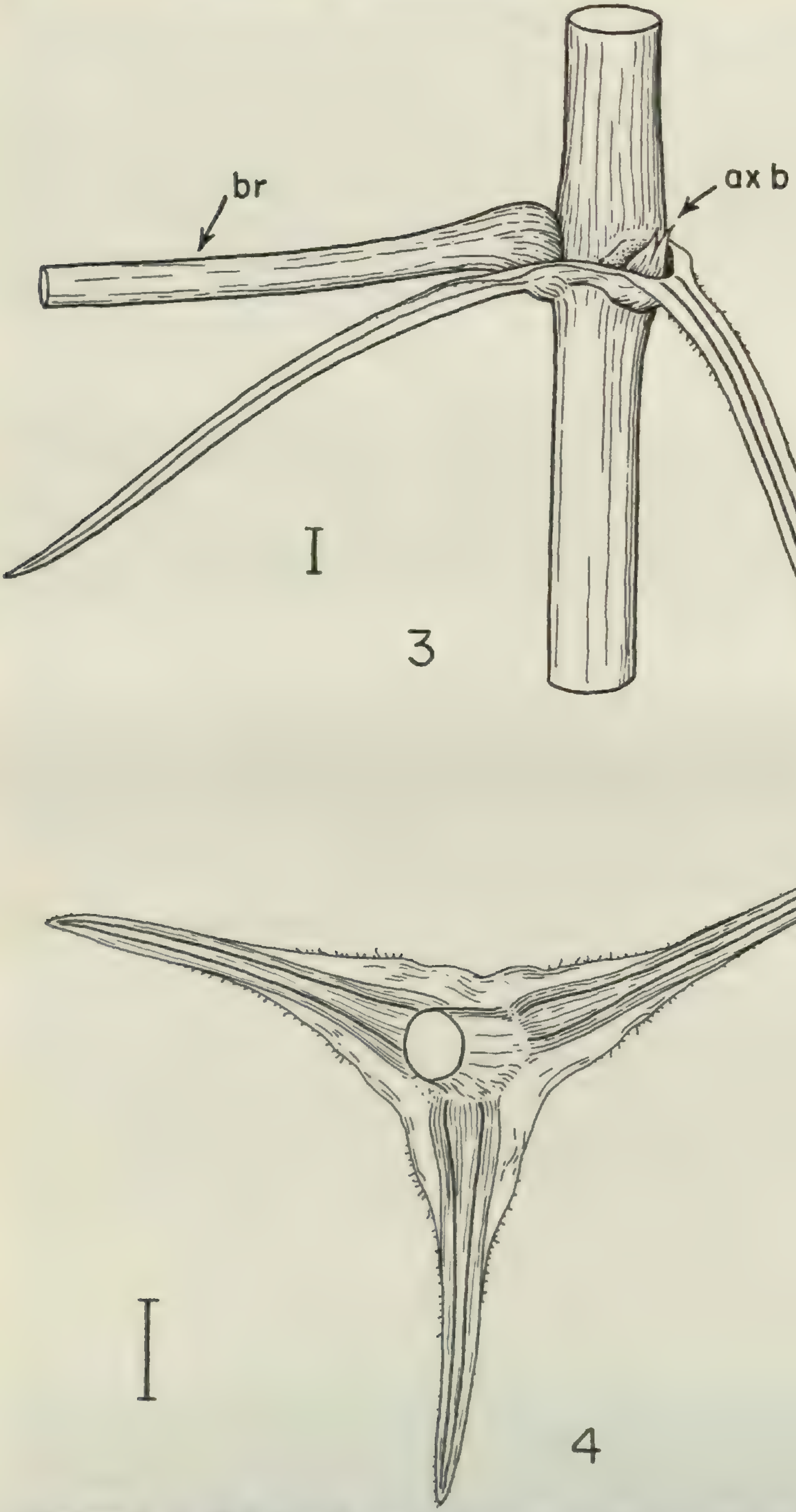
investigation, a number of successful preparations of divided nodal segments were obtained which show the contrast in nodal anatomy and venation which frequently occurs between members of a leaf-pair. A representative example of my results is shown in PLATE IV. In the three-veined leaf at the left (leaf A), the strong midvein is basally connected with the complementary bundle and the two lateral veins are joined independently to the stele in exactly the same manner as the traces of the two-veined leaf shown at the right (leaf B). Whether the midvein of leaf A represents the "foliar extension" of the complementary bundle or whether the latter simply provides a point of attachment for the midvein, are questions which can only be settled by appropriate ontogenetic studies.

An interesting, but unanticipated, result of my studies on *E. chilensis* was the discovery that in some leaves, the midvein terminates blindly at various levels in the lamina or sheath and hence fails to establish a connection with a complementary bundle (PLATE VI). Various types of "transitions" occur between leaves with basally connected midveins and those with "suspended" midveins. In some leaves, the basal connection between the midvein and the complementary bundle is tenuous and consists only of a file of slender tracheary elements (PLATE V: 11). Examples have also been found of three-veined leaves in which the midvein ends blindly in the nodal region between the points of attachment of the lateral traces (PLATE V: 12). Leaves with these venation patterns clearly seem to provide "connecting links" with the types of venation depicted in PLATE VI. Under high magnification, the basal end of a suspended midvein is usually slender and consists of a few elongated, helically-thickened tracheary elements (PLATE VII: 16).

This description of venation patterns in *Ephedra chilensis* may appropriately conclude with a few comments on the occurrence of transfusion tracheids. As shown in PLATES IV and V, transfusion tracheids are abundant in both two- and three-veined leaves. Very often, as shown in these illustrations, the vein-tips are "embedded" in a voluminous mass of transfusion tracheids. In the lower portion of the lamina, where the veins are well-separated, each vein is laterally flanked by continuous or interrupted files of conspicuous box-shaped transfusion tracheids (PLATE VII: 15). Cells of this type may be so abundant in the upper region of the leaf that the boundaries between adjacent veins are difficult or impossible to determine (PLATE IV: A; PLATE V: 12).

DISCUSSION

One of the most important conclusions of the present study is that the venation pattern is variable not only between the leaves of different species but, as in *Ephedra chilensis*, even between the members of the same whorl or pair of leaves (TEXT-FIG. 5; PLATE IV). This variability has received very little attention in the past (see "Review of Literature," p. 367). In most descriptions, the venation is said to consist of a pair of



FIGURES 3, 4. Variations in size and morphology of leaves in *Ephedra foliata* (*Barkley 32 Ir 2299*, UC). FIGURE 3, leaves with well-developed laminae and

free "parallel," veins which represent the upward extension of two leaf traces associated with a single gap. It is now clear, however, that the variation in venation pattern in *Ephedra* includes differences in both the number of veins — two or three — as well as the mode of termination of the veins in the lamina.

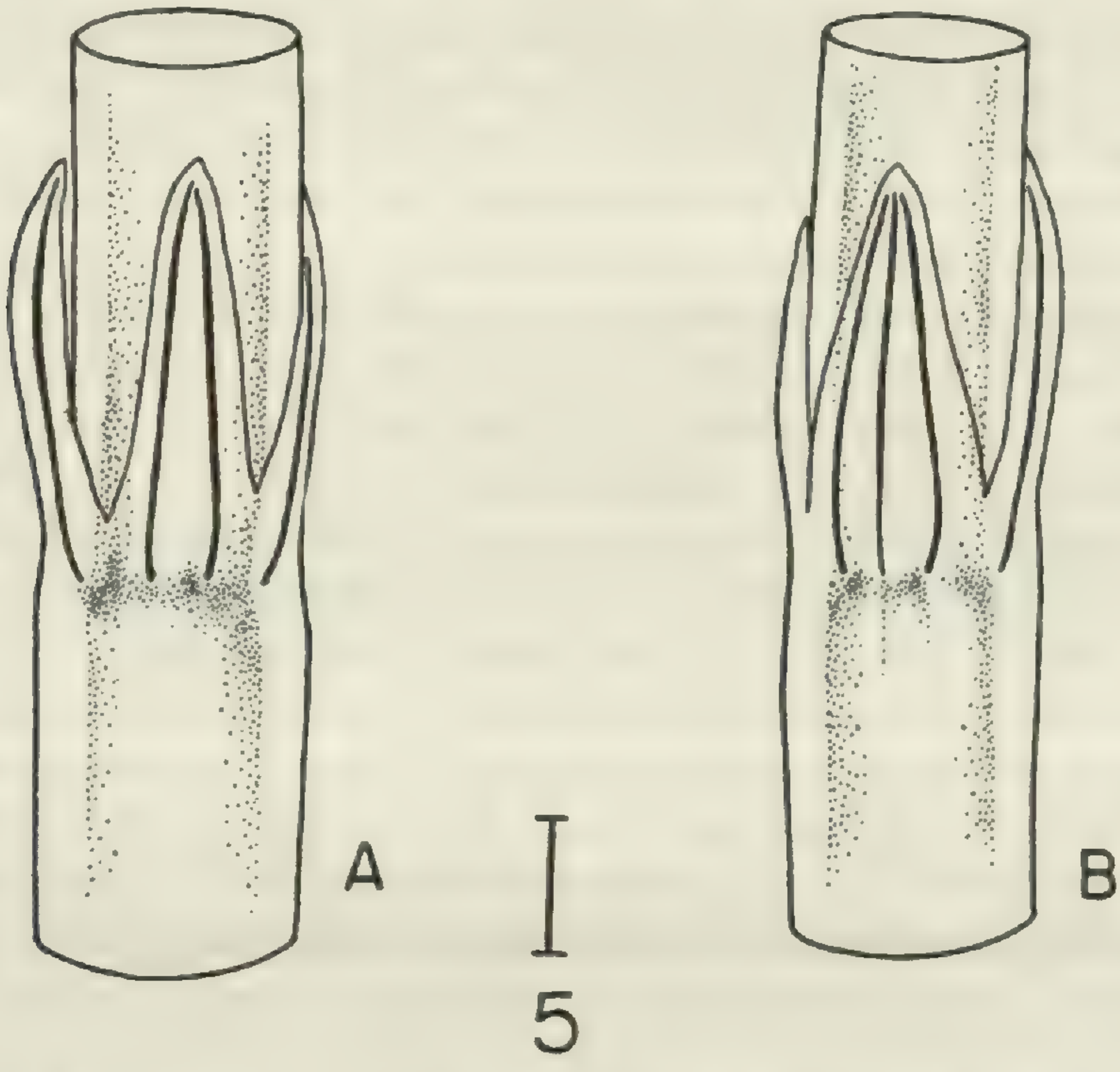


FIGURE 5, A, B. *Ephedra chilensis*. Variation in venation pattern among leaves of the same whorl. One leaf (B) is three-veined while each of the other leaves is two-veined (A). The scale between the drawings equals 1 mm.

In the three species which I have studied, "open venation" i.e. the free termination of the vein-tips, may occur in "rudimentary" as well as well-developed laminae, and probably represents the basic condition in the genus as a whole (TEXT-FIG. 1–5; PLATE I: 1, PLATE II: 5. 6). On the other hand, when transfusion tracheids, which are restricted to the borders of the xylem strands in open venation, subsequently develop *between* the veins, anastomoses are formed. As is shown in PLATE II, the degree of development of transfusion tracheids varies considerably and determines the fluctuation in the levels at which confluence of the veins takes place. In preparations of *Ephedra chilensis*, photographed by combining dark field illumination and transmitted light, the slender xylem-strands of each vein, in the lower part of the leaf, appear as dark lines

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weakly-connate sheaths; note open venation of leaf at right. *axb*. axillary bud, *br*, lateral branch. FIGURE 4, whorl of scale-leaves, detached from shoot and drawn from lower (abaxial) surface. Each leaf is vascularized by a pair of veins and is basally connected, by a prominent commissure, with adjacent leaves of the whorl. The scale at the side of each drawing equals 1 mm.

flanked by massive borders of refractive transfusion tracheids. At the points of lateral union between the veins, the interpolated files of transfusion tracheids are often clearly displayed (PLATES IV, V).

Quite apart from the anatomical contrasts between open and anastomosed venation, there remains the fundamental but difficult question of the significance of the three-veined type of leaf vasculature which occurs in *Ephedra chilensis*. My investigations demonstrate, in the first place, that there is no correlation between phyllotaxis and the number of traces and veins. Pairs or whorls of leaves may be uniformly two-veined, the predominant condition in *E. chilensis*, or one of the leaves at a node may be three-veined (TEXT-FIG. 5; PLATE IV). In my opinion, the reason for this apparently erratic fluctuation in vein-number is obscure, although Monoyer (1937, 1938, a, b, c) has proposed an ingenious explanation for the three-veined pattern in his study of several species of *Ephedra*. In *E. fragilis* var. *campylopoda*, Monoyer (1937) reported that *all* the leaves are consistently three-veined. The absence of a midvein in the leaves of the other species is the result, according to his view, of the failure of the median leaf trace to complete its extension into the leaf. Using the terminology adopted in the present paper, the so-called "complementary bundle," shown in PLATE III, corresponds in position to Monoyer's median leaf trace. From a theoretical point of view, Monoyer concluded that the three-veined pattern is "primitive" whereas a leaf with two veins represents a derived condition which results from the "acrolysis" (i.e. the atrophy) of the median trace (Monoyer 1938 b, p. 60). In his own words, "the bundles absent in the leaves are recovered in the stem in the form of acrolysed strands." (Monoyer 1938 c, p. 64).

Although Monoyer's theory is appealing because of its simplicity, I have found no evidence to support it. If the complementary bundle in the internode represents an incompletely developed median leaf trace, one might expect the occurrence of a "transitional" condition in which the median trace extends *for a short distance* into the leaf sheath. But I have never observed a venation pattern of this sort. On the contrary, the presumptive "arrest" in the development of the midvein occurs in the leaf itself rather than at the node, and is illustrated by appendages in which a median vascular strand terminates blindly at some level in the lamina or sheath (PLATE V: 12; PLATE VI). The venation pattern depicted in PLATE V: 12, suggests that the formation of tracheary elements in the midvein may occur *basipetally* and that the patterns shown in PLATE VI simply represent various degrees in the extent of such basipetal differentiations. This idea, however, because of the absence of ontogenetic data must be considered for the present as entirely speculative.

In angiosperms with unilacunar two-trace nodes the midvein of a foliar appendage may be formed by the union of a pair of central strands which arise as branches of the leaf traces (Bailey 1956). This type of transition from an even to an odd number of major foliar strands was not observed in *Ephedra chilensis*. In the three-veined leaves of this species, the midvein is an independently attached strand, interpolated between the lateral

traces and veins of the leaf (PLATE IV: A). Although the phylogenetic significance of this condition in such a gymnosperm as *Ephedra* is at present an enigma, it is interesting that in *Gnetum Ula*, both the scale-leaves and foliage leaves are vascularized by an odd number (5–7) of discrete leaf traces (Rodin & Paliwal 1970). Direct comparisons between the nodal anatomy of *Gnetum* and *Ephedra*, however, are of questionable value because of the obscure phylogenetic relationship between the two genera (Pearson 1929, p. 143; Eames 1952, p. 97).

There is a great need for a more comprehensive study of leaf venation in *Ephedra* than was possible in the present exploratory survey. The only known examples of three-veined leaves occur in *E. chilensis* and *E. fragilis* var. *campylopoda* which are assigned by Stapf (1889, p. 35) to "Tribus *Antisyphiliticae*" and "Tribus *Scandentes*," under the Section PSEUDOBACCATAE. If Stapf's classification is followed, it is evident that the taxonomic and phylogenetic significance of a trifasciculate type of foliar vasculature in *Ephedra* is an open question pending the results of further comparative studies. Stapf's scholarly monograph, frequently overlooked by modern investigators, describes in detail the leaf morphology and geographical distribution of 31 species of *Ephedra* and provides the essential basis for future surveys of nodal anatomy and venation in this genus.

[POSTSCRIPT TO ORIGINAL MANUSCRIPT]

Professor P. Marten's (1971) treatise, "Les Gnétophytes," came to my attention after the present paper had been completed. He takes the position that the morphological reduction of the leaf in *Ephedra* also involves its vascular system. This, he states, consists of two parallel collateral endarch veins which neither branch nor reunite in their course through the leaf. Although he notes (p. 21) that Monoyer (1937) had reported the occurrence of three-veined leaves in *E. fragilis*, he refrains from making any comment on the possible morphological or phylogenetic significance of this "divergent" pattern of venation.

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EXPLANATION OF PLATES

PLATE I

FIGURES 1–4. Variations in venation patterns of two-veined leaves of *Ephedra*. FIGURE 1. Free termination of veins near apex of leaf of *E. foliata* (*Barkley 32 Ir 2299*, UC). FIGURE 2. Leaf from same herbarium specimen as FIGURE 1, showing apical union between the two veins. FIGURE 3. *E. foliata* (cult. UC Bot. Garden) showing union, some distance below leaf-apex, of the two closely approximated veins. FIGURE 4. *E. altissima* (cult. USDA Plant Intro. Station, Chico, Calif.) showing confluence of the two veins distal to leaf-apex. All figures, × 11.8.

PLATE II

FIGURES 5–8. Details of vein structure in leaf-apices of *Ephedra foliata*. FIGURE 5. Apex of one member of leaf-whorl shown in TEXT-FIG. 4. Note conspicuous transfusion tracheids. FIGURE 6. Apex of leaf shown in PLATE I: 1. Each vein is bordered by abundant transfusion tracheids. FIGURE 7. Apex of leaf shown in PLATE I: 2. The vein-tips are united by a central mass of transfusion tracheids. FIGURE 8. Apex of leaf shown in PLATE I: 3. The two vein-tips are laterally merged, forming a single massive xylem-strand. Note cluster of prominent hairs developed at apex of lamina. All figures, × 62.

PLATE III

FIGURE 9. *Ephedra chilensis*. Cleared and stained longitudinal half of a nodal sector showing the independent attachment of the two leaf traces (*lt*), the nodal girdle composed of transfusion tracheids (*tr*) and the mode of termination at the node of the complementary bundle (*cb*). Note strands of fibers between the two veins of the leaf. × 92.

PLATE IV

FIGURE 10, A, B. *Ephedra chilensis*. A pair of cleared, stained leaves, separated by means of a longitudinal cut through the node and photographed by using a combination of dark field illumination and transmitted light. One leaf (A) is three-veined, with the median vein basally attached to the complementary bundle whereas the other member of the pair (leaf B) is two-veined. Note massive development of transfusion tracheids near the apices of both leaves. × 21.5.

PLATE V

FIGURES 11, 12. Three-veined leaves of *Ephedra chilensis*, photographed with a combination of dark field and transmitted light. FIGURE 11. Leaf showing a very attenuated connection between the median leaf vein and the complementary bundle. The three vein-tips merge with the transfusion tracheids near the leaf apex. FIGURE 12. Leaf illustrating the *blind termination* of the midvein between the bases of the two lateral traces. Note massive development of transfusion tracheids in upper part of lamina. × 26.

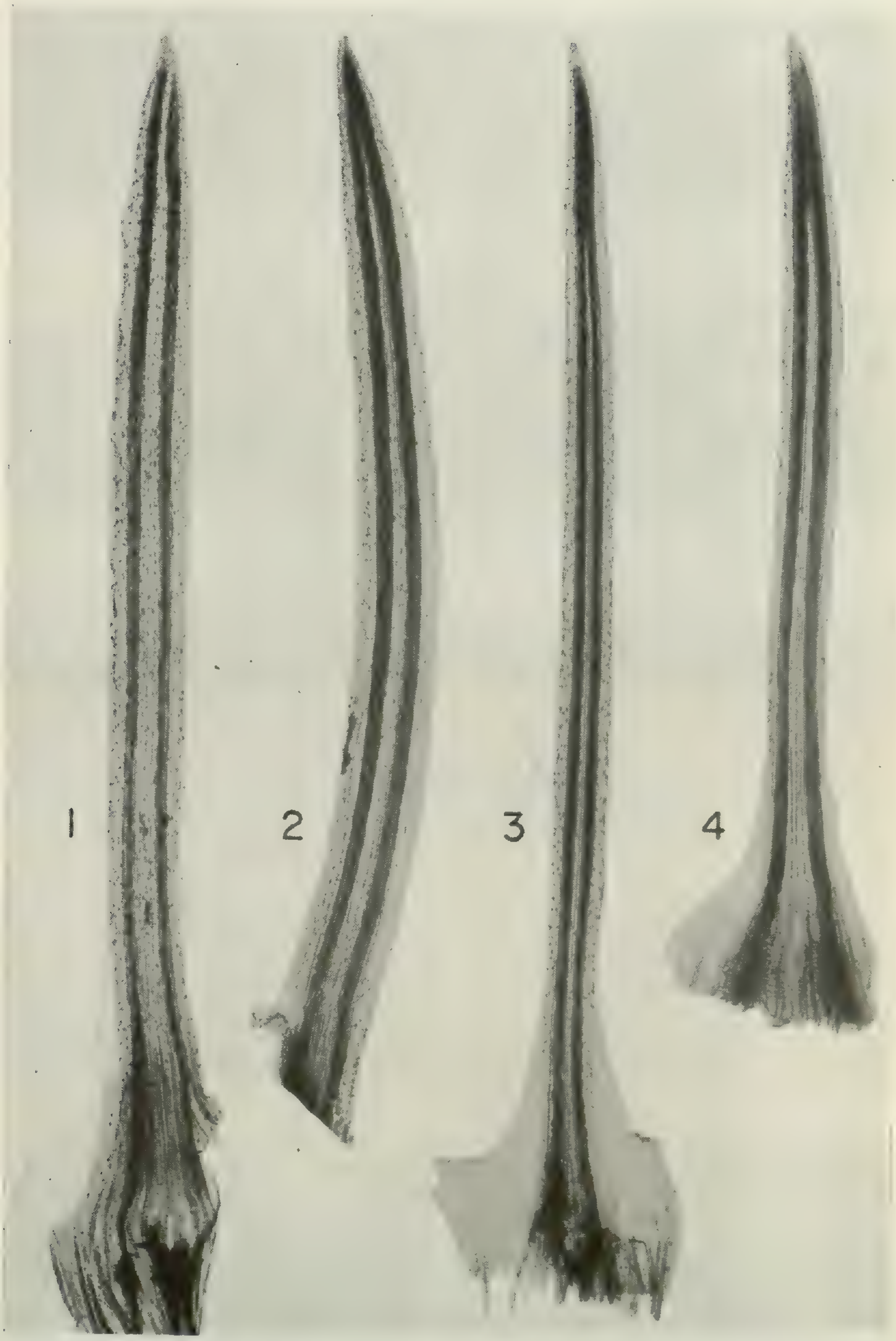
PLATE VI

FIGURES 13, 14. Leaves of *Ephedra chilensis* with blindly-terminating midveins, photographed by the combined use of dark field and transmitted light.

FIGURE 13. A detached leaf, showing the termination of the well-developed median vein in the lower part of the leaf sheath. Note transfusion tracheids between midvein and each lateral vein in upper part of lamina. FIGURE 14. Half of a longitudinally divided nodal sector, showing a discrete midvein ending blindly in base of lamina, and the connection of the lateral traces with the stele. Note the refractive appearance of the stomata in the lower portions of both photomicrographs. × 26.

PLATE VII

FIGURES 15, 16. Detailed structure of leaf veins of *Ephedra chilensis*. FIGURE 15. Small sector of lamina of leaf depicted in PLATE IV, A, showing large transfusion tracheids associated with each of the three veins. FIGURE 16. Structure of the blind termination of a suspended midvein. Note the slender tracheary elements of the blind ending and the abundant transfusion tracheids flanking the lateral veins. × 92.



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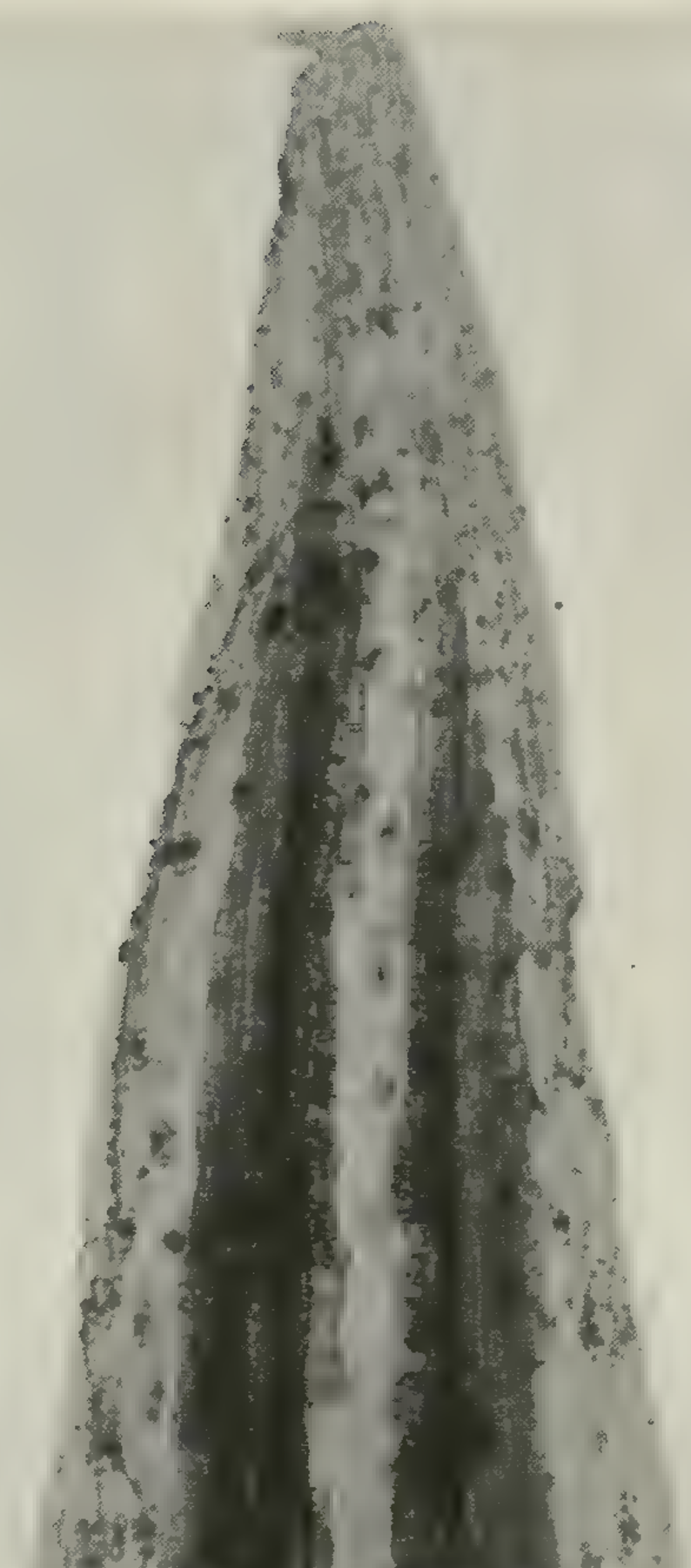
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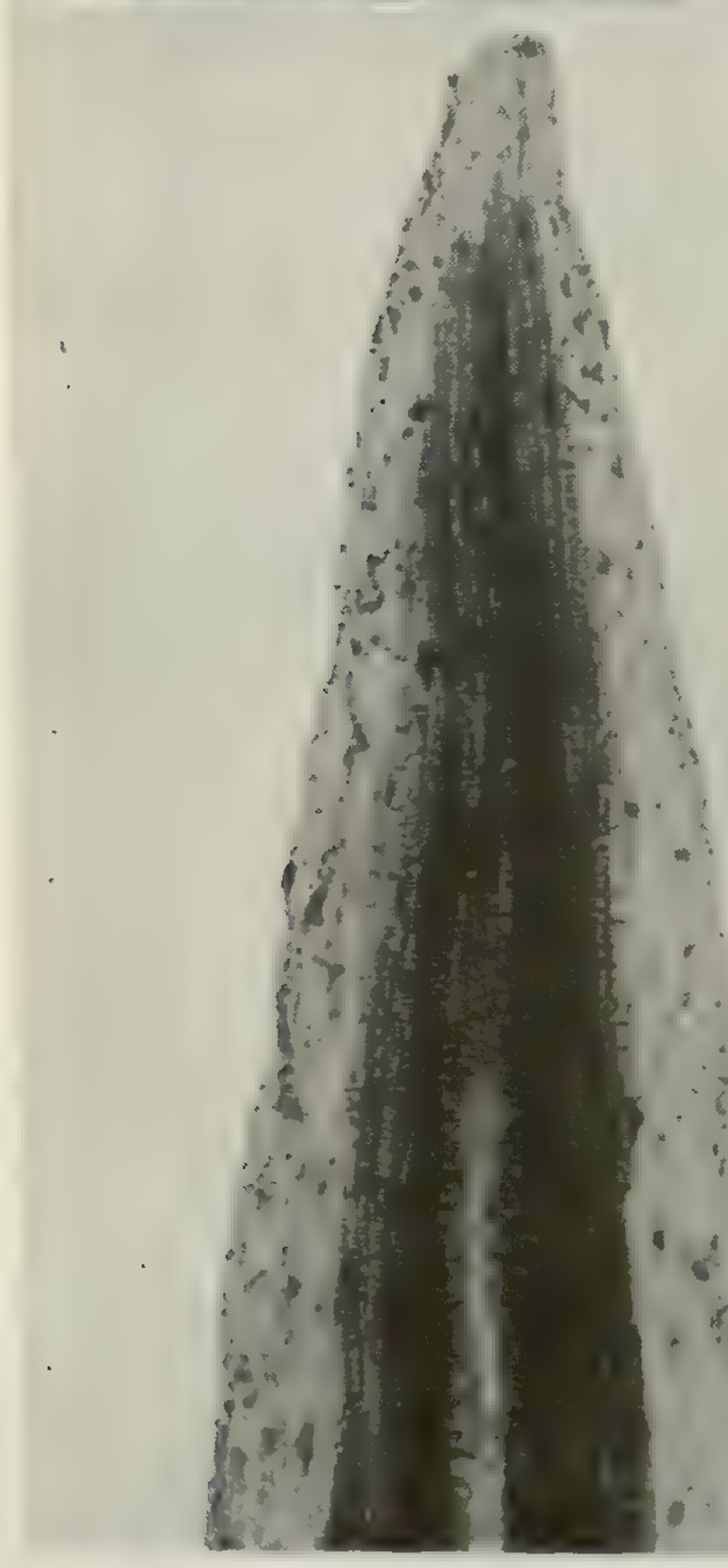
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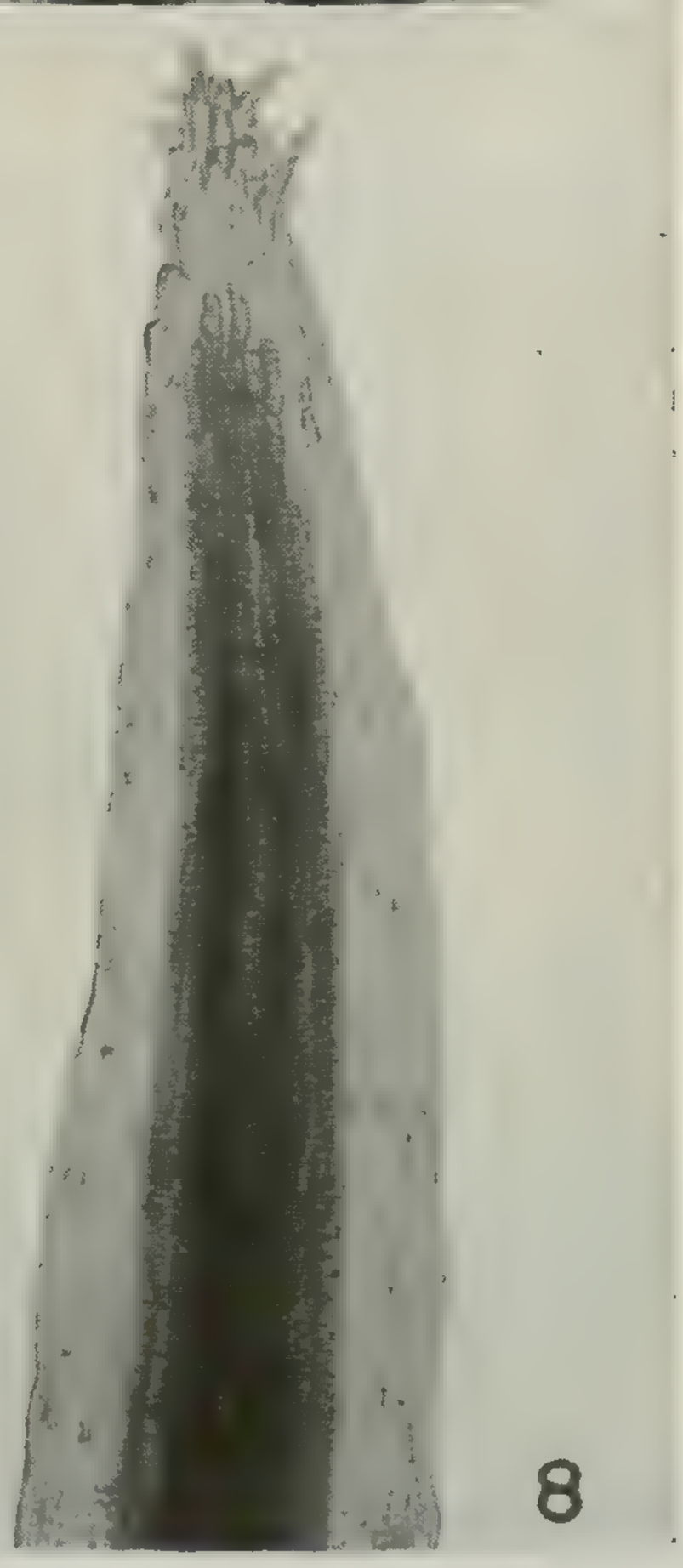
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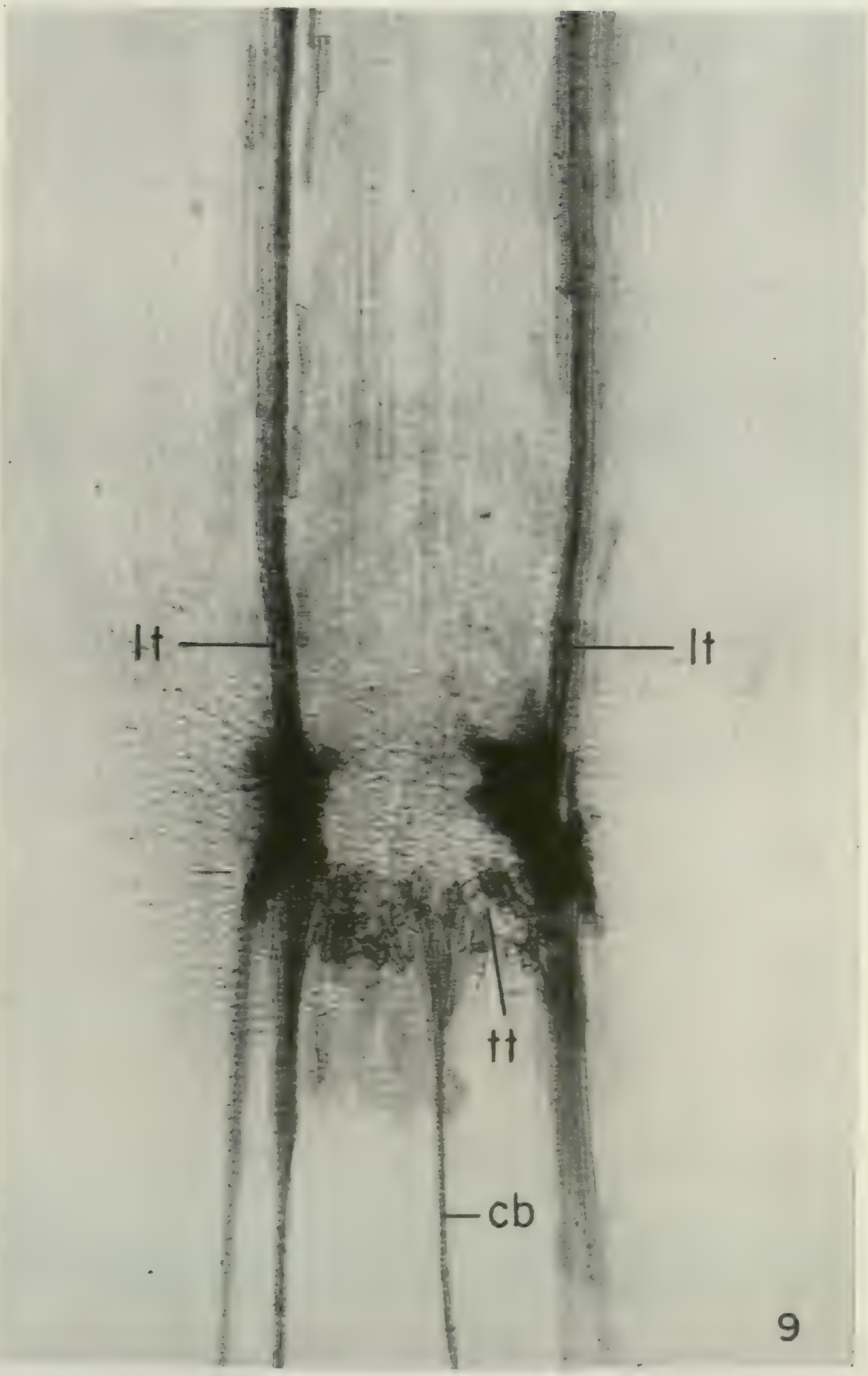

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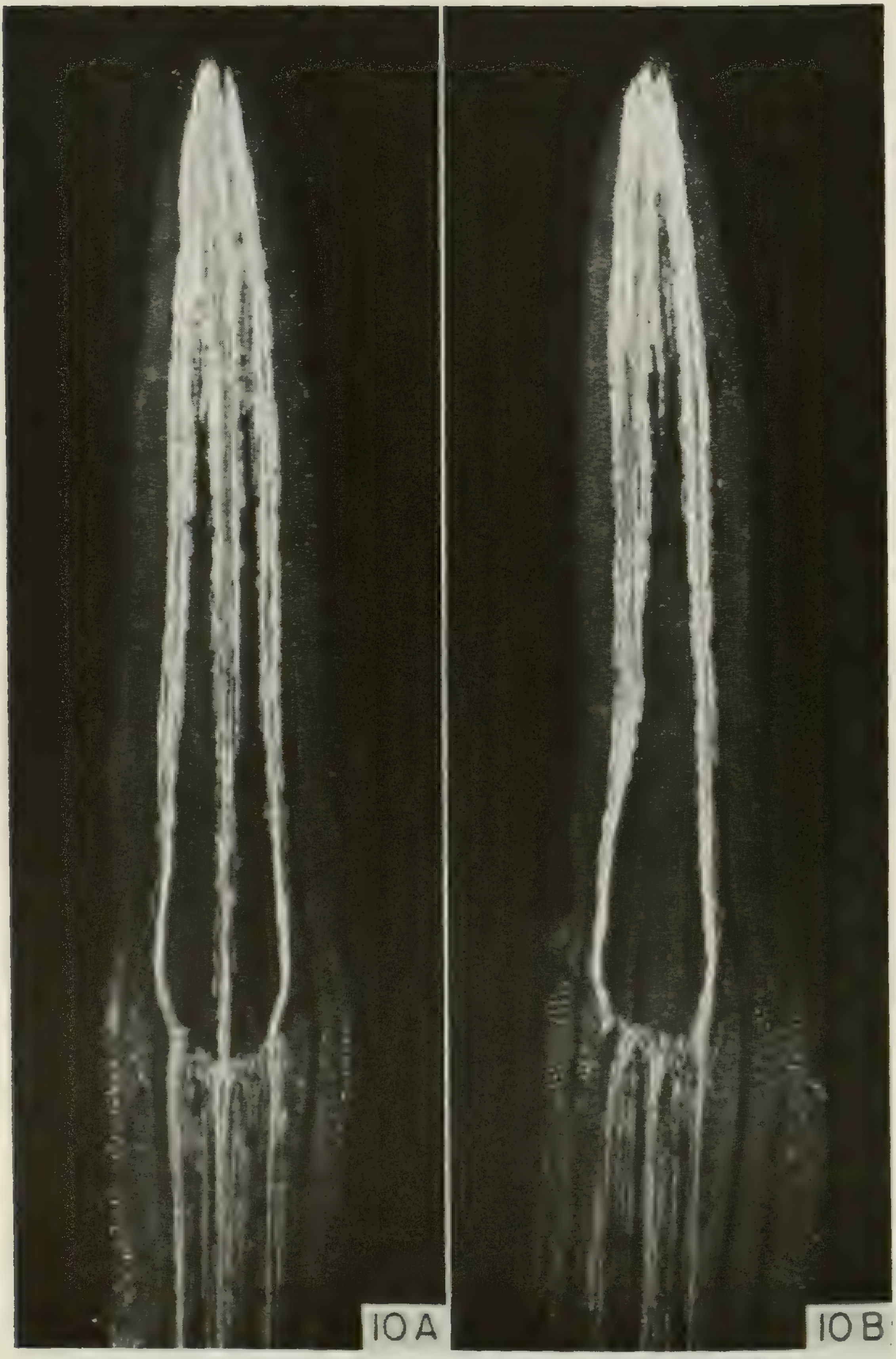

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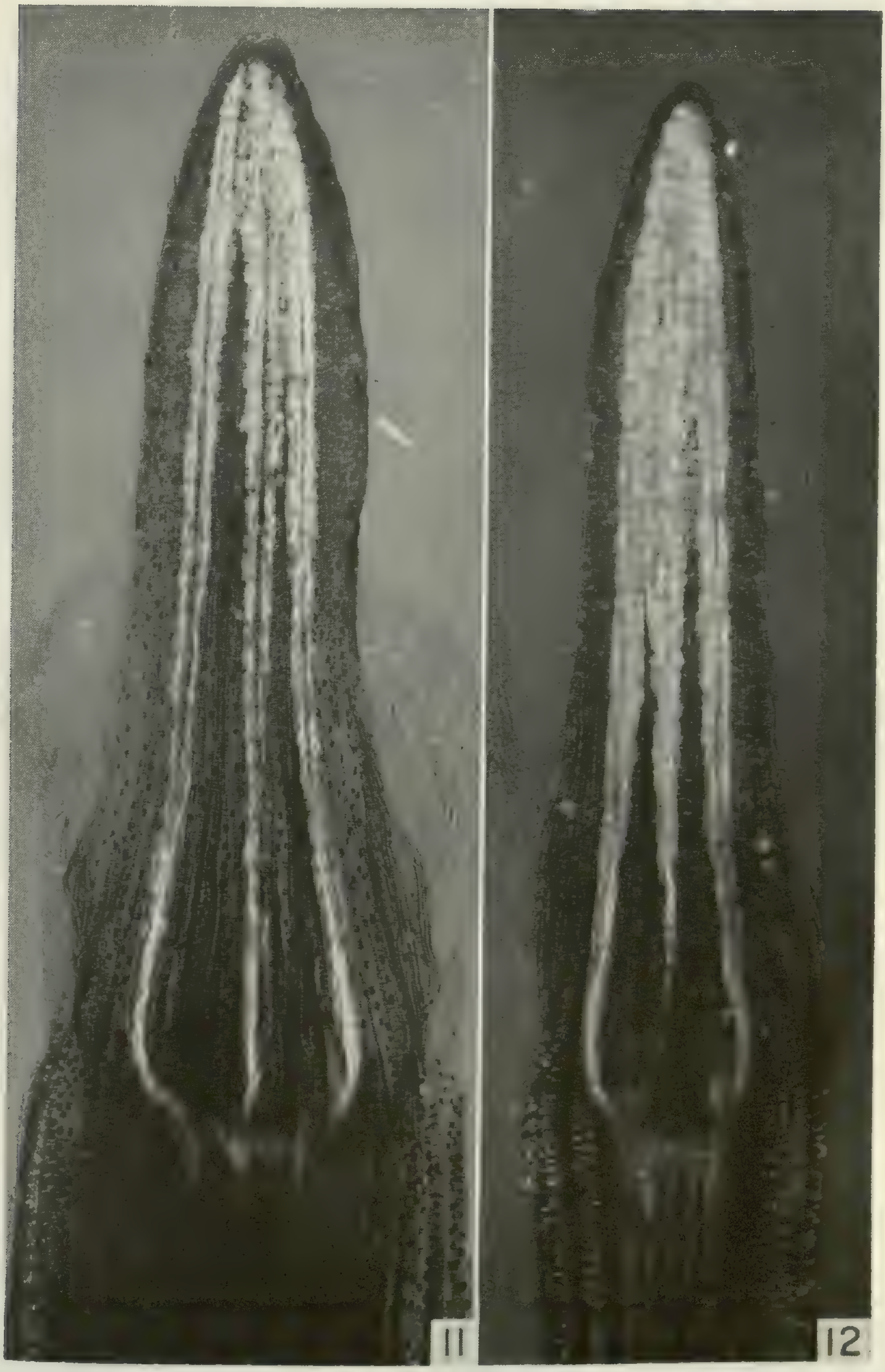

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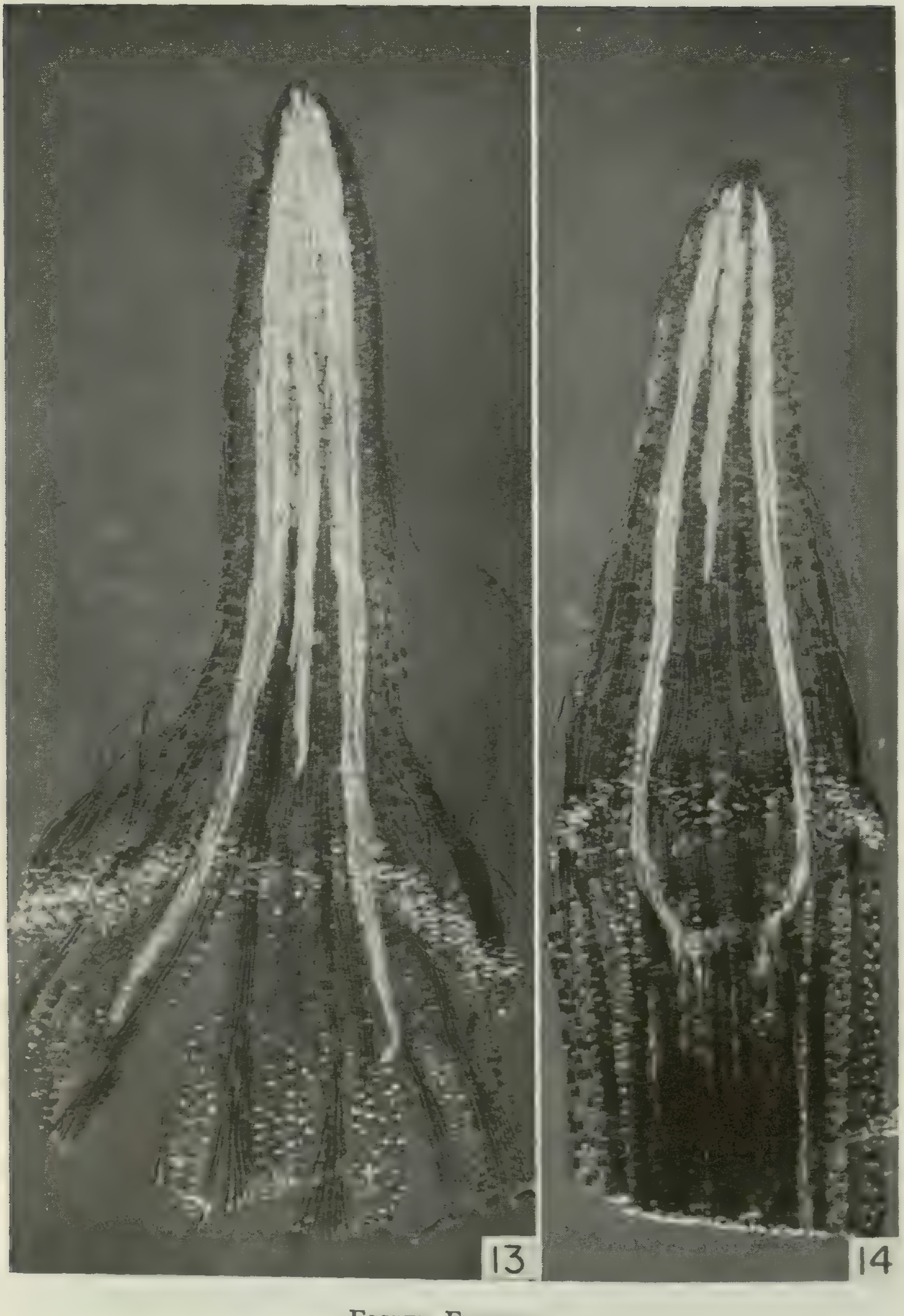

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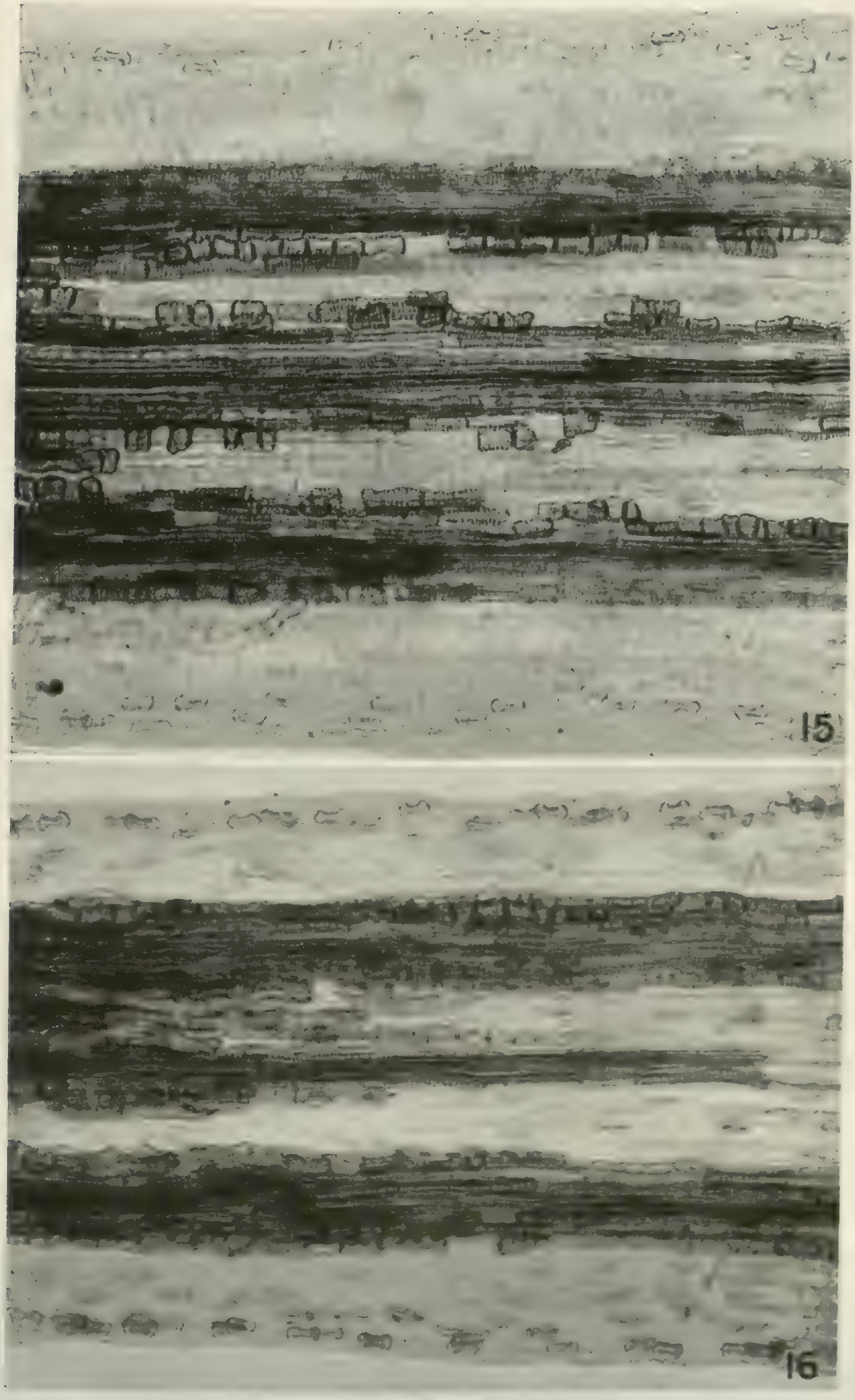

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DIOECISM IN CITHAREXYLUM (VERBENACEAE)

P. B. TOMLINSON AND PRISCILLA FAWCETT

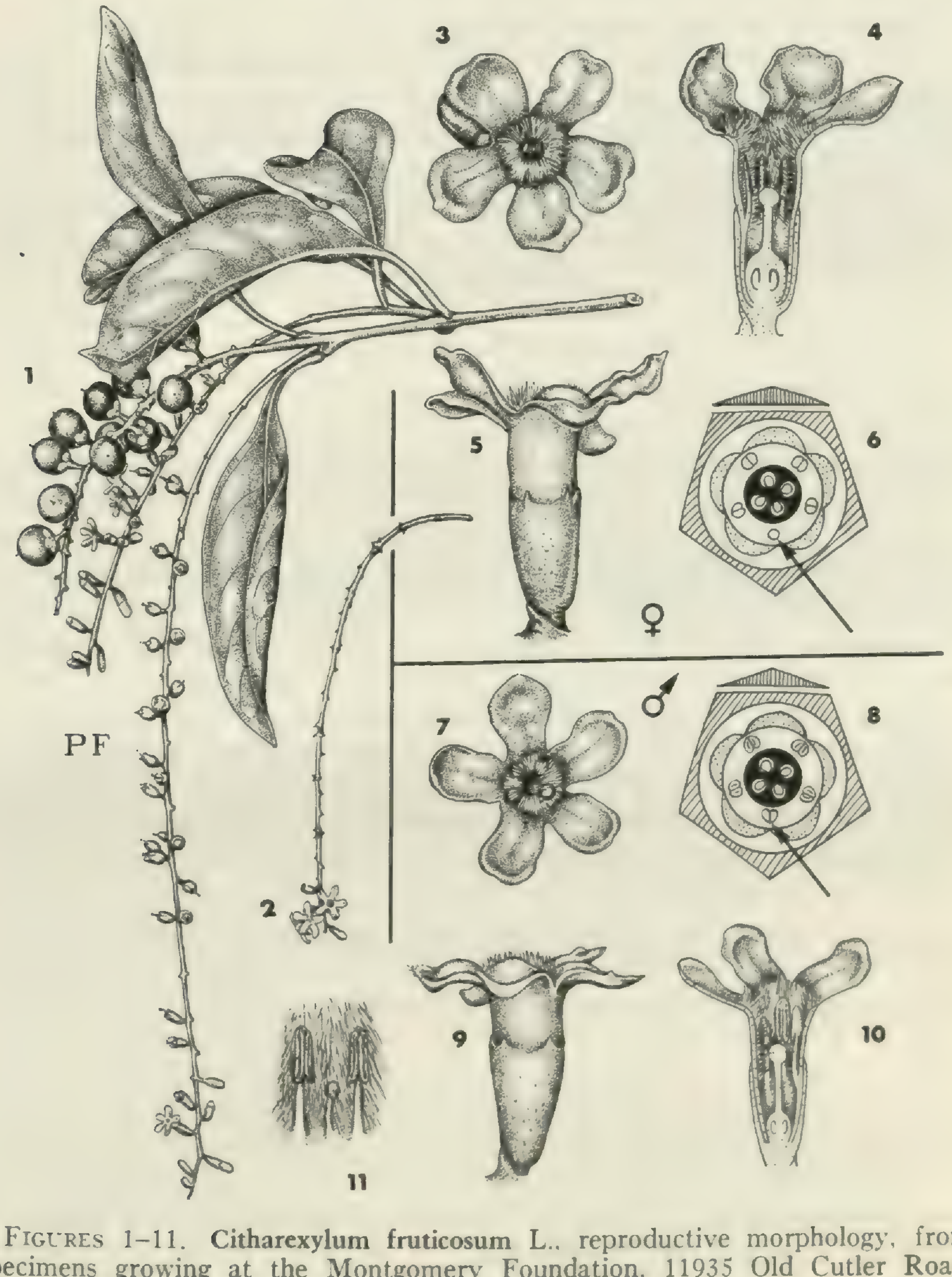
OUTBREEDING MECHANISMS ARE A feature of perennial plants (Stebbins, 1950 p. 165 *et seq.*) and their high incidence in trees is well known. This high incidence is related to the evolutionary advantages of outcrossing in terms of genetic flexibility. In continuing studies of the distinctive woody flora of South Florida it is evident that the majority of species have some simple and obvious mechanism for outcrossing such as dioecism, self-incompatibility as suggested by heterostyly, and other kinds of morphological polymorphism. Field study is revealing further examples among species which have hitherto been thought to have perfect flowers.

The present article refers to such an example in *Citharexylum fruticosum* L. ("Fiddlewood"). *Citharexylum* L. is a genus of some 100 species in Central and South America. The flowers seem largely to have been described as "perfect" (e.g. Sargent, 1894). *Citharexylum fruticosum* itself is widely distributed in the Caribbean area and a number of varieties have been described (Moldenke, 1959). In South Florida it is scattered in pinelands and hammocks on the Florida Keys and northward with a limited coastal distribution. The species tends to be a pioneer in recently burnt pineland and persists in more or less closed hammock communities which are the climax communities in many fire-free areas. The species shows distinct weedy tendencies and is not uncommon on disturbed sites. From this ease of spread and existence in natural communities it is an evident member of the native flora.

Descriptions of this tree in floras and other manuals dealing with this part of the United States (e.g. Chapman (1897), Sargent (1894), Small (1933). West and Arnold (1946)) or those which refer to it in other parts of its range (e.g. Britton and Millspaugh (1920), Léon and Alain (1957), Little and Wadsworth (1964), Moldenke (1954)) suggest, directly or indirectly, that flowers are perfect. In South Florida, at least, it is dioecious. This observation has been overlooked because the flowers in the two sexes are very similar and casual examination of herbarium specimens would not reveal the constant differences shown in field populations.

OBSERVATIONS

Phenology and Sexuality. *Citharexylum* begins to flower in early summer in South Florida (May–June). The flowers are on slender pendulous spikes which are either terminal on or from the upper leaf axils of current-year shoots (FIGURE 1). During the summer months several generations of renewal shoots with flowering branches may be produced so that the flowering period is extended. Flowers, however, do not occur



FIGURES 1–11. **Citharexylum fruticosum** L.. reproductive morphology, from specimens growing at the Montgomery Foundation, 11935 Old Cutler Road, Miami. Florida 33156. 1, female flowering shoot; 2, male spike; 3–6, female flower; 3. from above, 4, in longitudinal section, 5, from the side, 6, floral diagram; 7–10, male flower; 7, from above, 8, floral diagram, 9, from the side, 10, in longitudinal section; 11, detail of abaxial staminode and two adjacent stamens in a male flower. Figs. 1 & 2, × 1/2; figs. 3–5 & 7, 9 & 10, × 3; fig. 11, × 5.

"throughout the year" as has been stated in several publications, all of which seem to have their origin in the description by Sargent (1894). The phenology and general growth pattern of this tree is very distinctive and requires detailed study, a statement which could be repeated for all the woody plants of South Florida.

Towards the end of summer, and subsequently when fruit set begins, the difference between male and female trees becomes obvious. Fruits enlarge on female trees; male trees remain barren and can be distinguished throughout the fruiting season (September–December) by the pendulous but empty inflorescences. This distinction is evident even earlier, since fertilized flowers on female spikes lose only their corollas but retain the calyx and developing pistil (FIGURE 1, below). Male flowers fall as a unit after anthesis so the base of the inflorescence axis becomes bare (FIGURE 2).

Trees identified as male and female and tagged in one year retain their same sexuality in the following year.

Flowers. Superficially, flowers in the two sexes are identical (FIGURES 3–10). Each flower has a tubular, 5-toothed calyx which usually splits down one side. The corolla is tubular with 5(–6) more or less equal petal-lobes although the members of the adaxial pair are often somewhat larger than the three abaxial lobes. This tendency to zygomorphy is most pronounced in the stamens. There are 5 stamens or staminodes in each kind of flower but the adaxial one (indicated by the arrow in FIGURES 6 and 8) is usually distinctly different from the other 4; it is almost always smaller and it may be so reduced as to be represented by a mere vestige (FIGURE 11). In the male flower the 4 abaxial stamens are always fertile; dehiscence is introrse and the large pollen grains adhere into a relatively conspicuous mass. The adaxial stamen may contain pollen, even though it is reduced, but often it is vestigial, as in FIGURE 11. In the female flower the stamens are always sterile and the microsporangial tissue remains brown and never produces pollen. Such staminodes never dehisce.

The ovary appears to be equally well developed in both sexes (FIGURES 4 and 6; 8 and 10) with 4 equal ovules, one in each pseudoloculus. The stigma is more or less bilobed but the length of the style is somewhat variable, especially in the male flower. Usually the stigma is at about the same height as the stamens. There is no evidence that the ovules in the male flowers are functional since we have never seen fruits on male trees. The reason for this abortion of seemingly well-formed ovules is worthy of more detailed investigation.

Pollination. Flowers are sweet-scented during the day and nectar is secreted at the base of the ovary tube. Since the pollen is sticky it is evident that the flowers are insect pollinated but we have made no observations on the kinds of insect visitors. The mouth of the corolla tube is more or less occluded by a dense outgrowth of uniseriate multicellular hairs (FIGURES 3 and 7) and an insect probing for nectar would certainly touch both stigma and pollen mass. Self-fertilization of male flowers would seem to be quite easy.

Fruit set on female trees is very abundant but there seems to be a high incidence of fruits with aborted embryos.

CONCLUSION

It seems evident from these morphological observations that *Citharexylum fruticosum* is dioecious and it may seem remarkable that such a simple observation could have escaped the attention of botanists. However, this is a general reflection on how poorly the tree flora of South Florida has been investigated by field workers.

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NOTES ON WEST INDIAN ORCHIDS, II *

LESLIE A. GARAY AND HERMAN R. SWEET

During the preparation of the orchid manuscript for the *Flora of the Lesser Antilles* by Richard A. Howard of Harvard University, we have noted several nomenclatorial changes and have found a *Dichaea* species yet undescribed. Since the actual floristic presentation is not designed to incorporate new changes or descriptions of new species, our findings are presented here.

Elleanthus cephalotus Garay & Sweet, nom. nov.

BASIONYM: *Bletia capitata* R. Br. in Ait. Hort. Kew. ed. 2. **5:** 206. 1813.
SYN.: *Elleanthus capitatus* (R. Br.) Rchb.f. ex Cogn. in Urb. Symb. Antill. **6:** 561. 1910; Stehlé, Fl. Descr. Antill. Fr. **1:** 176. 1939. TYPE: West Indies, without proper locality. Introduced by Sir Joseph Banks in 1795 and flowered at Kew Gardens (BM).
Evelyna capitata Poepp. & Endl. Nov. Gen. ac Sp.Pl. **1:** 32. 1836.
Elleanthus capitatus (Poepp. & Endl.) Rchb.f. in Walp. Ann. Bot. Syst. **6:** 475. 1862; Schultes in Am. Orchid Soc. Bull. **25:** 387. 1956. TYPE: Peru, near Pampayaco. *Poeppig s.n.*! (W).

It is most unfortunate that the well-known descriptive name of *Elleanthus capitatus* has to be changed. This species has been described twice; first as *Bletia capitata* R. Br. and later as *Evelyna capitata* Poepp. & Endl. Recognizing that *Elleanthus* is the correct generic name, Reichenbach transferred *Evelyna capitata* to that genus. Cogniaux having found that *Bletia capitata* and *Evelyna capitata* were one and the same, because of the same specific epithet, he wrongly combined Robert Brown's epithet with Reichenbach's transfer. Because the specific epithet 'capitata' is preoccupied in *Elleanthus*, the transfer of *Bletia capitata* necessitates the new name proposed above.

Eltroplectris calcarata (Sw.) Garay & Sweet, comb. nov.

BASIONYM: *Neottia calcarata* Sw. Fl. Ind. Occ. 3: 1413. *t.28*. 1804. TYPE: Dominican Republic, without proper locality. *Swartz s.n.* (S).
SYN.: *Pelexia setacea* Lindl. Gen. and Sp. Orch. Pl. 482. 1840; Cogn. in Urb. Symb. Antill. **6:** 327. 1909.
Centrogenium setaceum (Lindl.) Schltr. in Beih. Bot. Centralbl. **37**(2): 453. 1920; Schultes in Am. Orchid Soc. Bull. **25:** 387. 1956. TYPE: Brazil. Rio Doce. *Prince Maximilian Wiedens s.n.*! (M, W).

We have examined a large series of specimens from the entire area of distribution, and have found that the margin of the lip may vary from

* Continued from Jour. Arnold Arb. **50:** 462–468. 1969.

entire to erose-denticulate or to almost fimbriate. Hence, *Neottia calcarata* and *Pelexia setacea* merely represent the two extremes in a single variation pattern.

Pleurothallis ophioglossoides (Jacq.) Garay & Sweet, comb. nov.

BASIONYM: *Epidendrum ophioglossoides* Jacq. Enum. Syst. Pl. 29. 1760, based on *Helleborine ophioglosso similis*, Plum. Cat. 9. 1703, and Icon. Burm. *t. 176, f.3.* 1759, not *Epidendrum ophioglossoides* Jacq. Sel. Stirp. Am. Hist. 225. 1763. TYPE: Martinique, without proper locality. *Plumier s.n.* (P). Holotype is Plumier's original drawing.

SYN.: *Specklinia floribunda* Lindl. Gen. and Sp. Orch. Pl. 9. 1830. *Pleurothallis floribunda* (Lindl.) Lindl. in Bot. Reg. **28:** misc. p. 73. 1842, not Poepp. & Endl. 1836; Rolfe in Kew Bull. 277. 1893; Cogn. in Urb. Symb. Antill. **6:** 421. 1909; Stehlé, Fl. Descr. Antill. Fr. **1:** 205. 1939; Hodge in Lloydia **17:** 213. 1954. TYPE: Martinique, without proper locality. *Sieber 206!* (K, W).

When Jacquin described *Epidendrum ophioglossoides* in 1760, he based his description on Plumier's polynomial of 1703 as well as on Plumier's drawing published subsequently by Burmann in 1759. Three years later, Jacquin published a new description of *Epidendrum ophioglossoides* without any reference to his 1760 paper, which he prepared from one of his own collections and which he assumed to be identical with Plumier's plates. Fortunately Jacquin's collection of that particular plant is in the British Museum. We have examined this specimen and it represents *Stelis scabrida* Lindl. A closer examination of Plumier's drawing immediately brings into focus the error in Jacquin's judgment, for Plumier's drawing is a true *Pleurothallis*, generally known as *P. floribunda* (Lindl.) Lindl.

Swartz in his *Observationes Botanicae* 332. 1791, already called attention to Jacquin's misidentification: "Plantae Plumieri & Jacquini certe distinctae. . . . Jacquini vero ad E. trigoniflorum (prodr. p. 125.) pertinet, affirmante planta Ipsius in Museo Banksiano serata." Notwithstanding his own observations, when he established the genus *Stelis* in 1800, Swartz followed Jacquin in proposing the new combination, *Stelis ophioglossoides* with his own *E. trigoniflorum* in synonymy. This mistake has been carried through to today for *Epidendrum ophioglossoides* became the conserved type of the genus *Stelis*. To prevent the transfer of over 1,000 species of *Pleurothallis* into the genus *Stelis*, the retypification of the genus *Stelis* will be published in a separate paper.

Octomeria apiculata (Lindl.) Garay & Sweet, comb. nov.

BASIONYM: *Pleurothallis apiculata* Lindl. Folia Orch. Pleurothallis 17. no. 88. 1859. TYPE: Venezuela, without proper locality. *Fendler 2155!* (K–L).

An examination of the type specimen of *Pleurothallis apiculata* has shown it to possess eight pollinia, one of the chief characters of the genus

Octomeria. A new and emended description of this species is given here for convenience.

Epiphyte. Primary stem or rhizome scandent, often covered with fibrous remnants of sheaths. Secondary stems rather slender, obliquely ascending, enclosed by 3 to 4 imbricating tubular scarious sheaths, up to 4.5 cm. long, proportionately (1:1) as long as or somewhat shorter than terminal leaf. Leaves coriaceous, narrowly ovate-elliptic to oblong-elliptic, acute, basally contracted into a short, up to 4 mm. long, petiole, including the petiole up to 6.5 cm. long and 7 mm. wide. Inflorescence fasciculate, 1- to 2-flowered. Flowers rather thin in texture, yellow, fragrant. Sepals similar, ovate to ovate-lanceolate, acute, 3–5 mm. long and 2 mm. wide. Petals ovate to rhombic-ovate, acute or acuminate, occasionally somewhat contracted below the tip, hence appearing apiculate, up to 4.5 mm. long and 1.5 mm. wide. Lip fleshy with distinct claw, 3-lobed; lateral lobes erect, more or less angular, midlobe ovate to oblong-ovate, obtuse or more or less 3-dentate at apex, margins erose-denticulate, disc provided with a pair of obliquely inserted fleshy lamellae at junction of midlobe and lateral lobes; whole lip up to 3 mm. long and 2 mm. wide. Column somewhat arcuate, up to 2 mm. long. Pedicellate ovary up to 4 mm. long.

General Distribution: Nicaragua, Costa Rica, Venezuela, Trinidad, Tobago, Grenada, and Guadeloupe.

Epidendrum latifolium (Lindl.) Garay & Sweet, stat. nov.

FIGURE 1.

BASIONYM: *Epidendrum nocturnum* var. *latifolium* Lindl. in Bot. Reg. **23**: *t. 1961*. 1837; Cogn. in Urb. Symb. Antill. **6**: 523. 1910; Stehlé, Fl. Descr. Antill. Fr. **1**: 144. 1939. TYPE: West Indies. Introduced and cultivated by *Paxton s.n.*! (K–L).

The strongly ancipitous stem, large elliptic leaves, sessile, 1-flowered inflorescence, and the flowers twice as large show no intergradation with *Epidendrum nocturnum* to which *E. latifolium* was formerly attached as a variety.

Epidendrum latifolium is known from the Greater and Lesser Antilles, Trinidad, and Venezuela.

Epidendrum secundum Jacq. Enum. Syst. Pl. 29. 1760, based on *Helleborine purpurea umbellata* Plum. Cat. 9. 1703 and Icon. Burm. 179. *t. 184, f.1*. 1759, not Jacq. Select. Stirp. Am. Hist. 224. *t. 137*. 1763.

SYN.: *Epidendrum fuscatum* Smith, Spicileg. Bot. fasc. **2**: 21. *t. 23*. 1792, *nom. superf*. TYPE: Martinique, without proper locality. *Plumier s.n.* (P). Holotype is Plumier's original drawing.

Epidendrum anceps Jacq. Select. Stirp. Am. Hist. 224. *t. 138*. 1763; Select. Stirp. Am. Hist., ed. icon. arch. pict. 108. *t. 208*. 1781; Boldingh, Fl. St. Eustat., Saba and St. Martin 41. 1909; Cogn. in Urb. Symb. Antill. **6**:

FIGURE 1. *Epidendrum latifolium* (Lindl.) Garay & Sweet. Drawn by Dorothy Allen.

516. 1910; Stehlé, Fl. Descr. Antill. Fr. 1: 134. 1939; Hodge in Lloydia 17: 205. 1954; Schultes in Am. Orch. Soc. Bull. 25: 387. 1956; Goodring, Loveless & Proctor, Fl. Barbados 112. 1965. TYPE: Martinique, without proper locality. *Jacquin s.n.* No specimen is known to us. Holotype is Jacquin's original illustration of which reproductions are cited above.

Epidendrum viridipurpureum Hook. in Bot. Mag. **65**: *t. 3666.* 1838.

Epidendrum anceps var. *viridipurpureum* (Hook.) Lindl. Folia Orch. Epidendrum 66. 1853; Cogn. in Urb. Symb. Antill. **6**: 518. 1910. TYPE: Jamaica, without proper locality. Imported and cultivated by *Horsfall s.n.*! (K).

It should be noted that Plumier's drawing upon which *Epidendrum secundum* is based and the description and drawing of *Epidendrum anceps* are identical in every respect. The fact that Jacquin described the same species twice within three years stems from his repeated misidentification of his own material when he superficially compared it with Plumier's drawings.

Pinelia Leochilus (Rchb.f.) Garay & Sweet, comb. nov.

BASIONYM: *Epidendrum Leochilus* Rchb.f. in Flora **48**: 277. 1865.

SYN.: *Pleurothallis tuberculata* Wright ex Griseb. Cat. Pl. Cub. 262. 1866, in syn. TYPE: Cuba, near Monte Verde. Flowers yellowish green or white, a red spot on the anther. *Wright 3346*! (AMES, W).

This exceedingly rare species has been collected recently for the first time in the Dominican Republic: on banks of Mao River, El Aguacate, La Leonor. *Liogier 13210*! (NY). Through this new collection we were able to determine the true generic status of this tiny plant.

Oncidium altissimum (Jacq.) Sw. in Vet.-akad. Stockholm Nya Handl. 21: 240. 1800, not of other authors.

BASIONYM: *Epidendrum altissimum* Jacq. Enum. Syst. Pl. 30. 1760. based on *Viscum radice bulbosa majus & elatius, delphinii flore ferrugineo guttato*, Sloane, Hist. Jamaica **1**: 250. *t. 148, f.1.* 1707, not Jacq. Select. Stirp. Am. Hist. 229. *t. 141.* 1763; ed. icon. arch. pict. 110. *t. 215.* 1781. TYPE: Jamaica, without proper locality. *Sloane s.n.*! (BM).

SYN.: *Epidendrum maculatum* Aubl. Hist. Pl. Guiane Fr. **2**: 825. 1775, based on *Helleborine maculosa, foliis aloës carinatis* Plum. Cat. 9. 1703 and Icon. Burm. *t. 178, f.2.* 1759, not *Oncidium maculatum* Lindl. 1841.

Epidendrum crispum Lam. Encycl. **1**: 186. 1783, not *Oncidium crispum* Lodd. 1832.

Oncidium maculatum (Aubl.) Urb. in Fedde Rep. **15**: 306. 1918. not *Oncidium maculatum* Lindl. 1841. TYPE: St. Vincent, without proper locality. *Plumier s.n.* (P). Holotype is Plumier's original drawing.

Oncidium luridum Lindl. in Bot. Reg. **9**: *t. 727.* 1823; Rolfe in Kew Bull. 278. 1893; Duss in Ann. Inst. Col. Marseille **3**: 600. 1897; Hodge in Lloydia **17**: 221. 1954; Schultes in Am. Orchid Soc. Bull. **25**: 391. 1956.

Oncidium guttatum Rchb.f. in Walp. Ann. Bot. Syst. **6**: 782. 1863. excl. syn.; Cogn. in Urb. Symb. Antill. **6**: 647. 1910; Kraenzlin in Pflanzenr. IV. 50. Heft **80**: 33. 1922; Stehlé, Fl. Descr. Antill. Fr. **1**: 248. 1939. TYPE: Introduced from South America and cultivated by *Griffin s.n.*! (K–L).

When Jacquin described *Epidendrum altissimum* in 1760, his description was based on a polynomial and an illustration in Sloane's Hist. Jamaica 1: *t. 148, f.1.* Three years later Jacquin redescribed and illustrated an entirely different plant as *Epidendrum altissimum* which he based on one of his own collections. We have examined the Sloane material in the British Museum and it represents the plant commonly known as *Oncidium luridum* Lindl., a plant very different from Jacquin's picture. Hence, the binomial *Oncidium altissimum* (Jacq.) Sw. is the correct name for this widespread plant. Although this same conclusion was reached by Fawcett and Rendle in 1910, they did not effect the necessary change.

On the other hand, the correct name for those plants which were named with the aid of Jacquin's plate of *Epidendrum altissimum* of 1763, is *Oncidium Wydleri* Rchb.f.

Dichaea Hookeri Garay & Sweet, sp. nov. FIGURE 2.

TYPE: Dominica, moist forests bordering Pegoua river in the vicinity of Deux Branches, Concorde Valley. *Hodge 3481!* (AMES).

Epiphytica, caespitosa; caulibus erectis vel pendentibus, compressis, foliatis, foliis patentibus, oblongo-ligulatis, acutis, mucronulatis, margine sub lente papilloso-ciliolatis; inflorescentiis unifloris; sepalo postico ovato-lanceolato, acuminato; sepalis lateralibus obliquis; petalis lanceolato-ellipticis, acuminatis; labello e cuneata basi anchoriformi, lobis acuminatis, retrorsis, antice rotundato cum apiculo minuto; ovario glabro.

Epiphytic, caespitose herbs up to 15 cm. tall. Stems erect to pendent, compressed, completely enclosed by imbricating leaf-bases. Leaves deciduous, length of leaves very uneven on stem, articulate, oblong-ligulate to linear-oblong, acute, indistinctly mucronate, the upper edge under lens finely papillose-ciliolate, up to 2.5 cm. long and 6 mm. wide. Inflorescence axillary, 1-flowered. Flower small, ringent, greenish to greenish yellow. Dorsal sepal ovate-lanceolate, acuminate, up to 5 mm. long and 2.5 mm. wide. Lateral sepals oblique, ovate-lanceolate, acuminate, up to 6 mm. long and 3 mm. wide. Petals lanceolate-elliptic, acuminate, up to 4.5 mm. long and 2.5 mm. wide. Lip from a cuneate base anchor-shaped with retrorse acuminate lobes, rounded in front with a small inconspicuous apicule in middle, up to 5 mm. long and 5 mm. wide when spread. Column cylindric. Ovary sessile, glabrous.

Flowers from March to July.

DISTRIBUTION. **Guadeloupe:** Mateliane, *Stehlé 456!* (AMES); Saralle. *Questal 4735!* (P); without proper locality, *L'Herminer s.n.!* (P); Hauteurs de Goyave, *Stehlé 961!* (AMES, NY). **Dominica:** La Chaudiere, Hampstead river. *Hodge 3509!* (AMES). **St. Vincent:** without proper locality, *Guilding s.n.!* (K). **Trinidad:** Aripo, *Broadway 2330!* (AMES); Mora forest, *R. O. Williams s.n.!* (AMES). **Island Margarita:** without proper locality, *J. R. Johnston 242!* (AMES). **Venezuela:** Guatopo, *Dunsterville 339!* (AMES).

Specimens referable to this species have been erroneously reported in the literature as *Dichaea Cogniauxiana* Schltr., *D. graminoides* (Sw.)

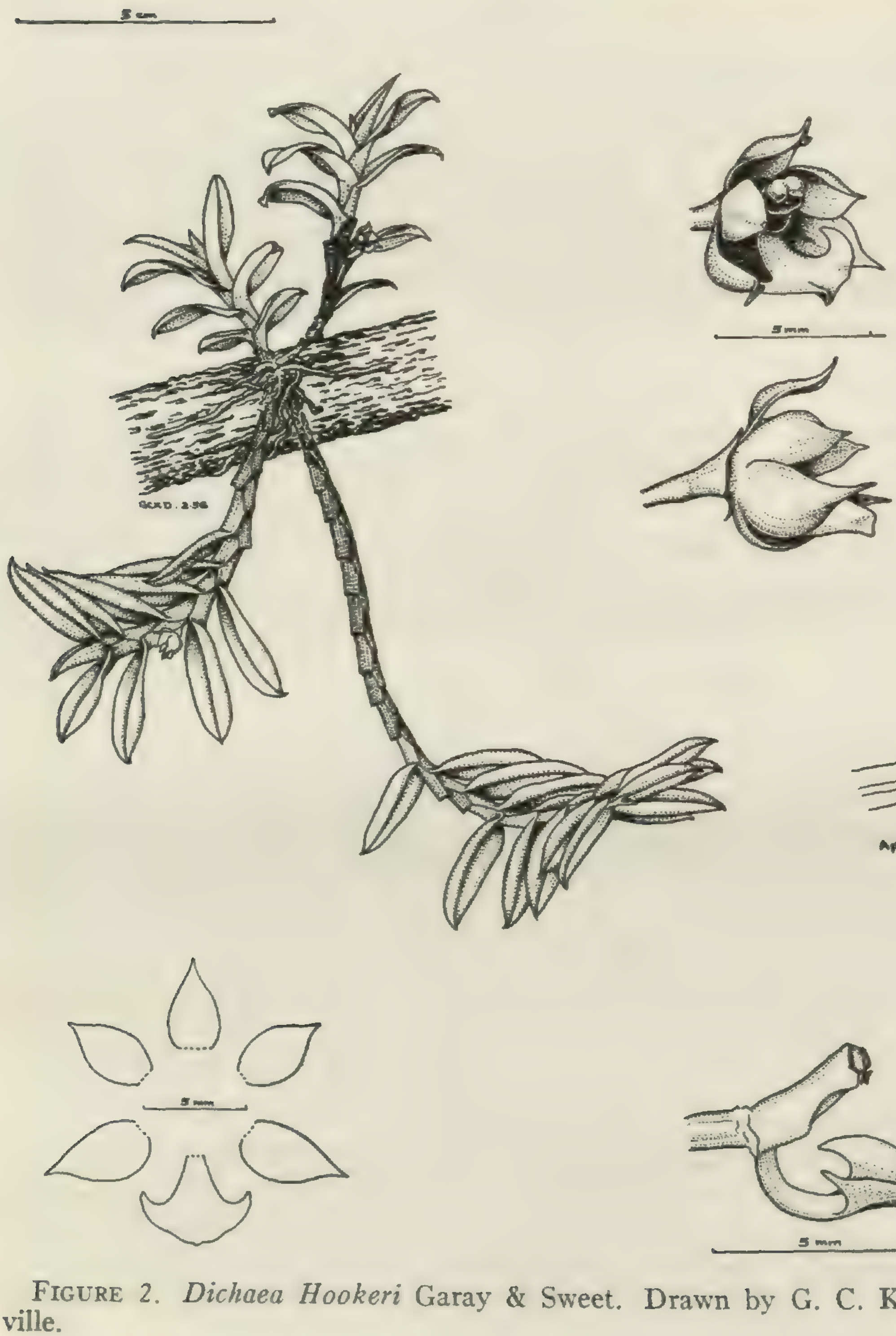
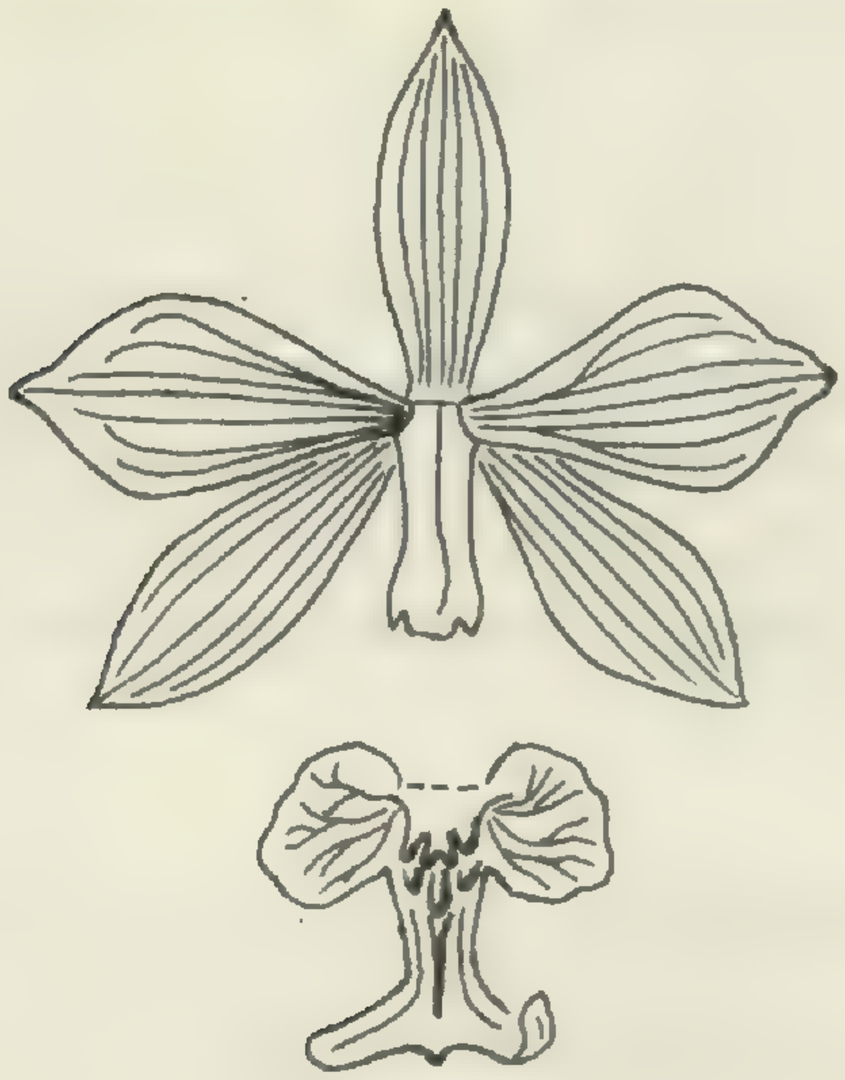
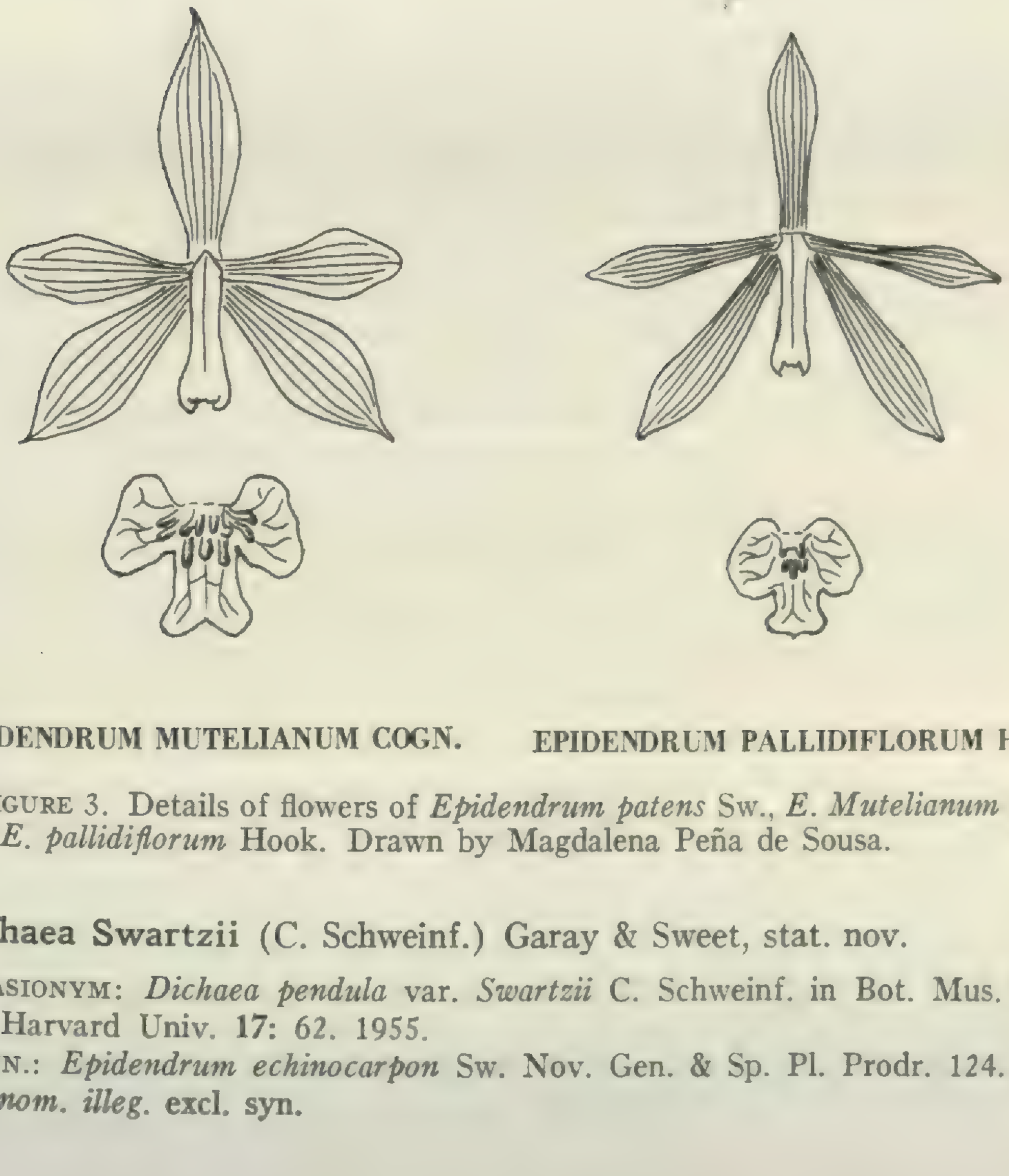


FIGURE 2. *Dichaea Hookeri* Garay & Sweet. Drawn by G. C. K. Dunsterville.

Lindl., *D. picta* Rchb.f., and *D. Rendlei* Gleason. The first illustration of *D. Hookeri* appeared in Hooker, Exotic Flora 3: *t. 196*. 1826, as *Isochilus graminoides* (Sw.) Lindl. Hooker's plate was based on the above cited collection from St. Vincent (not Trinidad as stated) and it is so marked on the herbarium sheet. Gleason's contention that Hooker's plate represented *D. Rendlei* is incorrect since a comparison of the original material from which the plate was prepared with that of the type of *D. Rendlei* has shown them to be distinct.



EPIDENDRUM PATENS SW.



EPIDENDRUM MUTELIANUM COGN. EPIDENDRUM PALLIDIFLORUM HOOK.

FIGURE 3. Details of flowers of *Epidendrum patens* Sw., *E. Mutelianum* Cogn., and *E. pallidiflorum* Hook. Drawn by Magdalena Peña de Sousa.

Dichaea Swartzii (C. Schweinf.) Garay & Sweet, stat. nov.

BASIONYM: *Dichaea pendula* var. *Swartzii* C. Schweinf. in Bot. Mus. Leafl. Harvard Univ. **17**: 62. 1955.

SYN.: *Epidendrum echinocarpon* Sw. Nov. Gen. & Sp. Pl. Prodr. 124. 1788, *nom. illeg.* **excl. syn.**

Dichaea echinocarpa (Sw.) Lindl. Gen. and Sp. Orch. Pl. 208. 1833, *nom. illeg.* excl. syn.; Duss in Ann. Inst. Col. Marseille 3: 596. 1897. TYPE: Jamaica, without proper locality. *Swartz s.n.*! (BM, S).

The original contention of Swartz that *Epidendrum echinocarpon* Sw. and *Epidendrum pendulum* Aubl. were one and the same species has been seriously questioned by Schweinfurth. In examining all of the available evidence we have found Schweinfurth's insight so justified that we recognize the West Indian material as a species separate from *D. pendula* (Aubl.) Cogn. from Guyana.

THE EPIDENDRUM PATENS COMPLEX

The three species, *Epidendrum patens* Sw., *E. Mutelianum* Cogn., and *E. pallidiflorum* Hook. have been thoroughly confused with one another in the literature. With the exception of the original diagnosis, all subsequent descriptions are mixtures and none may be used with certainty for identifications.

The original confusion was started by Lindley who misinterpreted Swartz's diagnosis of *E. patens* and applied it to one of the South American species of *Epidendrum*, namely *E. coronatum* Ruiz & Pav.

Cogniaux in preparing the orchid treatment for Urban's *Symbolae Antillanae* accepted Lindley's interpretation of *E. patens*, renamed the later homonym of *E. flavum* Mutel to *E. Mutelianum* Cogn. and included in this latter species all material now referable to the true *E. patens* Sw.

Stehlé in his treatment, *Les Orchidales*, *Flore descriptive des Antilles Françaises*, described and illustrated *E. Mutelianum* under the name of *E. pallidiflorum* and *E. patens* under *E. Mutelianum*.

We were fortunate to locate all three type collections. In order to clarify the distinctions among the three species, we are presenting an outline of their floral parts as a visual supplement to the following key:

1. Peduncle short, terete, up to 5 cm. long, surrounded by 1 to 4 lanceolate, basally imbricate, laterally compressed spathes; disc of lip plurituberculate at base. ..... *E. Mutelianum.*
1. Peduncle elongate, ancipitous, at least 10 cm. long, basally naked; disc of lip with a 3- to 5-dactylate plate at base. ..... 2.
2. Sepals elliptic; petals broadly ovate-rhombic, much wider than sepals; lip 3-lobed; midlobe linear-oblong with prominent diverging apical lobules; disc with a median keel. ..... *E. patens.*
2. Sepals lanceolate to linear-oblanceolate; petals linear-oblanceolate, much narrower than sepals; lip 3-lobed; midlobe subquadrate without apical lobules; disc without a median keel. ..... *E. pallidiflorum.*

ORCHID HERBARIUM OF OAKES AMES
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NOTES ON TIBOUCHINA AND CHARIANTHUS (MELASTOMATACEAE) IN THE LESSER ANTILLES

Richard A. Howard

Five species of *Tibouchina* are commonly recognized in the Lesser Antilles, but four of them are variously cited as to specific epithet and authors. The following notes are an attempt to clarify the nomenclature of the four species. The current typification of the genus *Charianthus* D. Don is in error, and a new combination is proposed for a second species.

Tibouchina ornata (Sw.) Baillon, Adansonia **12**: 74. 1876.

Melastoma ornata Sw. Prodr. 69. 1788 ("Jamaica," no specimens cited).
Rhexia strigosa Rich. Act. Soc. Hist. Nat. Paris **1**: 108. 1792.
Rhexia inconstans Vahl, Eclog. **1**: 37. 1796 (*nom. illeg.*).
Melastoma ciliata Desr. in Lam. Encycl. **4**: 49. 1797 (*Badier*, Guadeloupe).
Osbeckia ornata (Sw.) Sw. Fl. Ind. Occ. **2**: 647. 1798 (*Masson*, St. Kitts; *du Ponthieu*, Guadeloupe. Herb. Banks).
Rhexia ornata Rich. in Humboldt & Bonpland, Rhexies 69. *t. 26.* 1823.
Hephestionia strigosa Naud. Ann. Sci. Nat. ser. 3. **13**: 36. 1849.
Chaetogastra strigosa DC. Prodr. **3**: 134. 1828.
Pleroma strigosum Triana, Trans. Linn. Soc. **28**: 47. 1871.
Pleroma ornatum Triana, *ibid. t. 3, f. 31 p.* 1871.

This species is generally known as *Tibouchina strigosa*, and the authority for the name has been cited in a great variety of ways. The plant involved was first described by Olaf Swartz in his *Prodromus*, and cited as from Jamaica, with no collector indicated. In a subsequent treatment in the *Flora Indiae Occidentalis*, Swartz referred to the *Prodomus* treatment, did not mention Jamaica, and cited collections by Masson on St. Kitts, and by du Ponthieu on Guadeloupe. Such specimens are preserved in the Banks Herbarium at the British Museum (Natural History), and several collections are mounted on one sheet and are numbered. The specimen labeled #1 is selected as the lectotype, being that of du Ponthieu from Guadeloupe in flowering condition.

The Swartz epithet *ornata* has been cited in synonymy by many authors, but has not been adopted for the species as is necessary. Baillon did make the combination *Tibouchina ornata*, but used the basionym *Pleroma ornatum* Triana. Triana had published the name *Pleroma strigosum* in the text of his treatment on the Melastomataceae, and cited in synonymy "Osbeckia ornata Tuz. Fl. Ind. Occ. 647," which is apparently a typographical error for Swartz, Fl. Ind. Occ. 647. In the explanation of the plates in the same work on page 162, Triana refers to *Pleroma ornatum* Tri. One can assume he was correcting the name used earlier in the text, and was using the Swartz name as a basionym.

The correct citation of name and authority is *Tibouchina ornata* (Sw.) Baillon.

This species has been collected on Montserrat, St. Kitts, Guadeloupe, and Dominica, within the Lesser Antilles. Cogniaux (DC. Monogr. Phan. 7: 267. 1891) also cites under *Tibouchina strigosa* collections from St. Vincent by Anderson and Masson, and from "Guiana anglica ad Demerara" by Parker. Gleason (Brittonia 1: 156. 1932) has already suggested the Parker specimen might be of a cultivated plant and not native to the Guianas. Alexander Anderson was the director of the botanic garden on St. Vincent (1783–1811) and might have had the species under cultivation there. Recent explorations of the Soufrière on St. Vincent, the logical location for the natural occurrence of the species, have failed to produce "*T. strigosa*," but quantities of *Tibouchina cistoides* instead. The vegetation of the summit area of the Soufrière was destroyed in the eruption of the volcano in 1902. It is possible that the species might have been eliminated in that eruption except for the fact that it has not been reported from Martinique, where perhaps the same situation prevails on the slopes of Mt. Pelée. Masson is known to have collected on St. Kitts where the species occurs today, but not on St. Vincent.

Tibouchina chamaecistus (Naud.) Cogn., DC. Monogr. Phan. 7: 267. 1891.

Hephestionia chamaecistus Naud. Ann. Sci. Nat. ser. 3. **13:** 37. 1849.
Chaetogastra chamaecistus Griseb. Fl. Brit. W. I. Isl. 267. 1860.

The basionym for this combination is usually attributed to Grisebach, who cited the Naudin work at the generic level only. However, Naudin has used the specific epithet in his publication, and it is presumed that Grisebach implied a transfer and a new combination. The type specimen was collected by Mme. Rivoire on the slopes of Mt. Pelée in Martinique, the only known location for this species.

Tibouchina chironioides (Griseb.) Cogn., DC. Monogr. Phan. 7: 267. 1891.

Chaetogastra chironioides Griseb. Fl. Brit. W. I. Isl. 267. 1860.

Cogniaux made the combination indicated above; cited the species in his monograph; and referred to collections by Imray, Morris, Ramage, and to *Eggers 714*, all from Dominica. He did confuse subsequent workers, however, by also citing *Chaetogastra chironioides* Griseb. "part" in the synonymy of his *Tibouchina strigosa*. Karl Domin has already indicated (Acta Bot. Bohemica 9: 35. 1930) that Grisebach cited but a single collector, Imray, and although all of the Imray collections I have seen are clearly referable to this species, a specimen in the Gray Herbarium bears an old annotation in an unknown hand as "Chaetogastra strigosa."

Depauperate plants of *Tibouchina ornata* collected on Dominica led some scholars to associate *T. ornata* and *T. chironioides* as a single species,

judging from the annotations. The leaves of *Tibouchina ornata* are trinerved and ovate. The Imray collection, which is the type of *T. chironioides*, and such subsequent collections as *Eggers 714, W. H. & B. T. Hodge 1860, Wilbur et al. 8244* all have narrowly lanceolate leaves 6–7 mm. long and rarely exceeding 1 mm. in width. *Tibouchina chironioides* appears to be endemic to Dominica at altitudes of 1900 to 2100 feet.

Tibouchina longifolia (Vahl) Baill. ex Cogn., DC. Monogr. Phan. 7: 264. 1891.

Rhexia longifolia Vahl, Eclog. **1:** 39. 1796.

The author of this name is generally considered to be Baillon in Adansonia 12: 74. 1876, although other references and authors have been cited. Baillon did not make the combination, but only implied it, when he noted that *Pleroma* of Don should be included within a variable *Tibouchina*. For other species, such as *Tibouchina ornata* (Sw.) Baillon, he did cite a full basionym.

Pleroma longifolia Triana (Trans. Linn. Soc. **28:** 45. *t. 3, f. 31 n.* 1871) is based on *Rhexia longifolia* Vahl. The correct basionym appears to be cited first by Cogniaux as indicated, although he attributed it to Baillon. For accuracy the authority should be cited as Baillon ex Cogniaux.

This species is reported to occur from Bolivia to Venezuela, in Central America, the Lesser Antilles, and the Greater Antilles. The type is a collection of von Rohr from "America meridionali," probably the Guianas.

The genus *Charianthus* was established by David Don (Mem. Wernerian Soc. **4:** 327. 1823), at which time he cited three species, *C. coccineus* (L. C. Rich.) D. Don, *C. purpureus* D. Don, and *C. tinifolius* D. Don. In a monograph of the genus, W. H. Hodge (Contrib. Gray Herb. **135:** 115–133. 1941) indicated the "type species" to be *Charianthus corymbosus* (L. C. Rich.) Cogniaux. Since this species was not within the original material cited by D. Don, it cannot stand as the lectotype of the genus, and accordingly I select *Charianthus purpureus* D. Don, which is based on *Melastoma coccinea* Vahl, Eclog. 1: 48. 1796, not L. C. Richard, Act. Soc. Hist. Nat. Paris 1: 109. 1792.

Charianthus alpinus (Sw.) R. A. Howard, comb. nov.

Melastoma alpina Sw. Prodr. 71. 1788; Fl. Ind. Occ. **2:** 800. 1797.
Melastoma coccinea L. C. Rich. Act. Soc. Hist. Nat. Paris **1:** 109. 1792.
Charianthus coccineus (L. C. Rich.) D. Don, Mem. Wernerian Soc. **4:** 328. 1823.

David Don listed as the first species in his new genus *Charianthus, C. coccineus* (L. C. Rich.) D. Don, based on *Melastoma coccinea* L. C. Rich. However, he cited in synonymy *Melastoma alpina* Sw. giving as a reference only Flora Indiae Occidentalis 2: 800. Pages 641 to 928 of this work are said to have appeared in 1797 (Stafleu, Taxonomic Literature, Reg. Veg. **52:** 462. 1967). However, Swartz did refer to his earlier use

of the basic reference, his Prodromus 71. 1788. Don and subsequent authors have ignored this earlier valid basionym and a new combination is necessary.

The supporting specimen cited by Swartz was collected by du Ponthieu in the alpine mossy forest region of the Soufrière on Guadeloupe, and such a specimen is in the Banks Herbarium (BM).

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ON TROPICOS: flora ... type & distr

THREE NEW SPECIES OF ZANTHOXYLUM (RUTACEAE) FROM DARIEN PROVINCE, PANAMA

DUNCAN M. PORTER #0005452

LIKE MANY WIDESPREAD, species-rich, tropical woody genera, *Zanthoxylum* suffers from a lack of adequate collections in the herbarium. A few species are represented by numerous specimens, but for the vast majority there are few, one, or more often than that none. It is impossible to gain an adequate grasp of such a genus without examining a large suite of specimens from throughout its range; it is also impossible to have any understanding of specific relationships without doing so. Knowledge of *Zanthoxylum* is such that the relationships of the species described below from eastern Panama are obscure. Unfortunately, each is known only from the type collection.

Zanthoxylum eliasii D. M. Porter, sp. nov. *Zanthoxylo kellermanio* affinis, sed inflorescentiae ramis puberulis et folliculis maturis 3 vel raro 1 vel 4 differt. FIGURES 1 and 2.

TYPE. **Darién:** "Cerro Pirre, alt. 2,500–4,500 ft. Cloud forest and/or mossy forest. Spindly tree 4 inches DBH; fruits red." 9–10 August 1967, *J. A. Duke & T. S. Elias 13851* (MO, holotype; F, GH, isotypes).

Spindly tree; branchlets glabrous. Leaves alternate, odd-pinnate; petiole and the rachis together 15–32 cm. long, canaliculate above, minutely puberulent to glabrate; leaflets 7, opposite or subopposite, ovate to oval, abruptly acuminate apically, inequilateral and more or less rounded basally, the margins entire, subcoriaceous, pellucid-punctate throughout, minutely and sparingly puberulent on the veins below, 10–22 cm. long and 5.5–8.5 cm. wide, the petiolules canaliculate above, to 1 cm. long. Carpellate inflorescences stout, axillary, minutely puberulent, 7.5–16.5 cm. long and to 10 cm. wide in fruit. Carpellate flowers with the pedicels stout, minutely puberulent, 4–7 mm. long in fruit; sepals 5, triangular, less than 1 mm. long; carpels 3(–4), connate. Follicles (1–)3(–4), subglobose, sessile, more or less beaked, connate basally, punctate-glandular, glabrous, red at maturity, ca. 5 mm. in diameter; seeds subglobose, black, shiny, ca. 5 mm. in diameter.

This species is named for Dr. Thomas S. Elias, an avid student of the Rutaceae. *Zanthoxylum eliasii* appears to be related to *Z. kellermanii* P. Wilson of British Honduras, Guatemala, Honduras, and El Salvador. In Wilson's key to the genus in North America (N. Am. Fl. **25**: 178–180.

FIGURES 1 AND 2, Zanthoxylum eliasii D. M. Porter. 1, photo. of holotype specimen; 2, close-up of follicles.

FIGURES 3 AND 4, **Zanthoxylum jaimei** D. M. Porter. 3, photo. of holotype specimen; 4, close-up of follicles.

1911), which includes Panama, *Z. eliasii* would be determined as *Z. kellermanii*. However, the latter differs in having even-pinnate leaves, appressed-pubescent branches of the inflorescence, and 2 or 3 mature follicles.

Zanthoxylum jaimei D. M. Porter, sp. nov. *Zanthoxylo arborescenti* aemulans, differt foliolis ca. 9–11 et ramulis, rhachidibus, et inflorescentiae ramis puberulis. FIGURES 3 and 4.

TYPE. **Darién:** "Cerro Pirre, alt. 2,500–4,500 ft. Cloud forest and/or mossy forest. Apparently an armed tree; branch picked up off the ground." 9–10 August 1967, *J. A. Duke & T. S. Elias 13793* (MO, holotype).

Tree; branchlets armed with small brownish prickles, minutely puberulent. Leaves apparently odd-pinnate; petiole and the rachis together 3–10 cm. long, minutely puberulent, especially toward the base; leaflets ca. 9–11, opposite (?), elliptic to obovate, abruptly acuminate apically, inequilateral and cuneate basally, the margins crenulate, coriaceous, pellucid-punctate throughout, minutely puberulent, especially along the impressed midrib above and on the blade beneath, 25–65 mm. long and 13–27 mm. wide, the petiolules ca. 1 mm. long. Carpellate inflorescence minutely puberulent, the main branch armed with small brownish prickles, 15 cm. long in fruit. Carpellate flowers with the pedicels minutely puberulent, 1–2 mm. long in fruit; sepals 5, triangular, apiculate, minutely puberulent, less than 1 mm. long; carpels 3, free. Follicles 1, subglobose, beaked, shortly stipitate, punctate-glandular, glabrous, 3–4 mm. in diameter.

This species is named for Dr. James A. Duke, prodigious collector of Panamanian plants. The epithet *dukei* is not used because of the prior publication of *Fagara duckei* de Albuquerque (Publ. Inst. Nac. Pesq. Amazonia Bot. **27**: 6. 1968) from the Brazilian State of Pará. I agree with Brizicky (Jour. Arnold Arb. **43**: 80–83. 1962) and Hartley (op. cit. **47**: 171, 172. 1966) that *Fagara* L. and *Zanthoxylum* L. are congeneric. Thus the Brazilian species should be regarded as **Zanthoxylum duckei** (de Albuquerque) D. M. Porter, comb. nov.

In Wilson's key to *Zanthoxylum* (N. Am. Fl. **25**: 178–180. 1911), *Z. jaimei* would be determined as *Z. arborescens* Rose, from the Mexican states of Baja California, Sinaloa, and Jalisco. The latter has 3 to 7 leaflets, and the twigs, leaf rachises, and branches of the inflorescences are densely hispidulous.

Zanthoxylum pucro D. M. Porter, sp. nov. *Zanthoxylo bijugo* aemulans, differt ramulis et foliis glabris et inflorescentiis scabridiusculis. FIGURE 5.

TYPE. **Darién:** "Forest 1–4 mis. n. of Pucro. Armed tree 5″ DBH;

FIGURE 5, **Zanthoxylum pucro** D. M. Porter, photo. of holotype specimen.

flowers green." 22 June 1967, *J. A. Duke 13029* (MO, holotype; GH, isotype).

Tree, armed with prickles; branchlets glabrous. Leaves apparently odd-pinnate; petiole and the rachis together 44–53.5 cm. long, glabrous, more or less canaliculate above; leaflets apparently alternate, oblong, inequilateral, abruptly acuminate apically, oblique basally, the margins crenate, membranaceous, pellucid-punctate only at the bases of the crenations, glabrous, 6.5–17.5 cm. long and 3–6 cm. wide, the petiolules to 5 mm. long, winged. Staminate inflorescences congested, paniculate, terminal (?), scabridulous. Staminate flowers green in bud, the pedicels to 1 mm. long, scabridulous; sepals 5, broadly triangular, glandular-punctate, the margins hyaline, ciliate, imbricate, the 3 outermost larger, ca. 1 mm. long; petals 5, obovate, glandular-punctate, yellow (?), imbricate; stamens 5, the anthers sagittate; the filaments inserted on the disc; ovary ovoid, sharply 5-lobed and each lobe bilobed, glandular-punctate, glabrous, less that 1 mm. in diameter, star-shaped in cross-section, the styles 3, free. Follicles unknown.

Unfortunately, the type specimen was collected under circumstances of high temperature and high humidity, conditions not conducive to good preservation of plant materials. It is overgrown with fungi, and all the leaflets have fallen from the rachises. However, the material is sufficiently well preserved to show that it is unlike any other member of the genus yet described.

In Wilson's key to the genus in North America (N. Am. Fl. **25**: 178–180. 1911), *Zanthoxylum pucro* would be determined as *Z. bijugum* (Engler) P. Wilson, from Oaxaca, Mexico. However, the latter differs most obviously in having the twigs, foliage, and inflorescences densely pilose.

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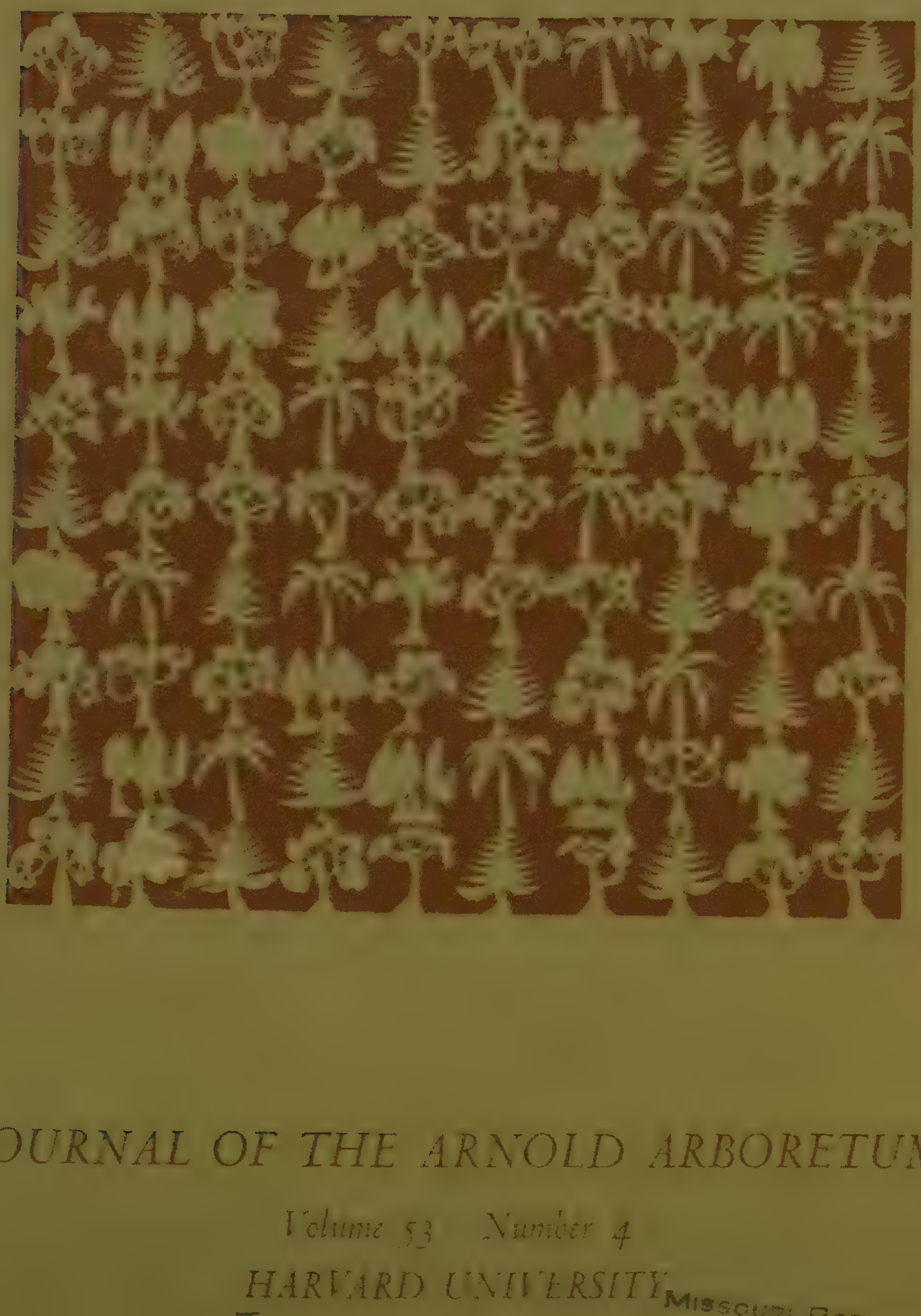

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COVER: A CENTURY OF TREES.

The cover design was planned and drawn by Karen [illegible]berger Velmure especially for the *Journal of the Arnold Arboretum* [illegible]ill be used during 1972 to celebrate the Centennial Year of the A[illegible]rboretum of Harvard University. The design consists of one hun[illegible]s representing the range and diversity of the collections of the A[illegible]um.

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THE GENERA OF SAXIFRAGACEAE IN THE SOUTHEASTERN UNITED STATES [1]

STEPHEN A. SPONGBERG

SAXIFRAGACEAE A. L. de Jussieu, Gen. Pl. 308. 1789, "Saxifragae," nom. cons.

(SAXIFRAGE FAMILY)

Variously pubescent annual [rarely biennial], or perennial often suffruticose or semisucculent herbs, unarmed or armed shrubs [small trees], or woody vines from fibrous roots (some producing rhizomes); herbs (subfam. Saxifragoideae) often reproducing vegetatively by stolons and bulbils. Leaves alternate, opposite (subfam. Hydrangeoideae), mostly basal, or clustered on short, lateral shoots (subfam. Ribesioideae), petiolate or sessile, stipulate or, more commonly, exstipulate; blades simple or pinnately [or palmately] compound, the leaf or leaflet margins entire or variously

[1] Prepared for a generic flora of the southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of the National Science Foundation (Grant GB–6459X, principal investigator, Carroll E. Wood, Jr.). This treatment follows the format established in the first paper in the series (Jour. Arnold Arb. **39:** 296–346. 1958). The area covered includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on plants of this area, with supplementary information in brackets. References that I have not seen are indicated by an asterisk. The literature listings given in this paper are by no means all-inclusive, particularly with regard to horticultural/agricultural references for the genus *Ribes*.

I am particularly indebted to Professor Wood for his patience, careful review of the manuscript, and help with taxonomic and editorial problems; to Dr. Elizabeth A. Shaw for translations of certain Russian references; to Dr. Lorin I. Nevling, Jr., for information concerning the Hydrangeoideae; to Dr. Bernice G. Schubert for her careful editing; and to Mrs. Nancy Dunkly for checking bibliographic citations and retyping much of the manuscript. The illustrations were prepared by a cohort of Generic Flora artists and represent the careful work of the late Dorothy H. Marsh, Rachel A. Wheeler, Arnold D. Clapman, Virginia Savage, and Karen Stoutsenberger Velmure. Materials used in the preparation of the illustrations have been kindly supplied by R. B. Channell, S. Leonard, N. G. Miller, R. E. Primack, the late H. F. L. Rock, D. H. Thomas, A. F. Tryon, R. E. Weaver, Jr., and K. A. Wilson, and collected by Dr. Wood and myself.

toothed, lobed, or cleft, the venation pinnately netted, palmate, or penniparallel; hydathodes often associated with the marginal teeth (subfams. Saxifragoideae and Ribesioideae). Flowers regular or occasionally irregular, perfect or imperfect (and the plants hermaphroditic, dioecious, polygamous, or polygamodioecious), or occasionally neuter (subfam. Hydrangeoideae), arranged in pedicellate, often bracteate racemes, cymes, panicles, or corymbs, or sometimes occurring singly. Calyx usually persistent, regular or occasionally irregular, of 4 or 5 or 7–10(12) sepals, the sepals valvate or imbricate in bud and almost always connate below, forming a shallow to deep, sometimes ribbed floral cup with reflexed or ascending calyx lobes, the insertion of corolla and androecium hypogynous to epigynous; a glandular, nectar-secreting disc or annular ring often developed at the base of the floral cup, sometimes extending over the surface of the ovary. Petals usually as many as calyx lobes, occasionally lacking, or variable in number, imbricate or valvate in bud. Stamens as many as or twice as many as the calyx lobes or sometimes numerous [up to 100 or more] (subfam. Hydrangeoideae), occasionally differentiated into staminodia and functional stamens (subfam. Parnassioideae); filaments [sometimes with lateral appendages] tapering to the subcordate to linear, basifixed, 4-sporangiate (2-loculate at anthesis) anthers; pollen 2- or 3-celled when shed. Gynoecium 2- or 3-, 5–7-, or 8–10(12)-carpellate, apocarpous or syncarpous, the styles usually as many as the carpels and free, occasionally united, sometimes forming a massive stylar column; stigmas capitate, occasionally with radiate stigmatic surfaces; ovary superior and free to inferior and adnate to the floral cup, 1-, 2-, 4-, 5–7, or 8–12-loculate with numerous anatropous, 1- or 2-integumented, crassinucellar or tenuinucellar ovules on axile or parietal placentae. Fruit a loculicidal, septicidal, or apically dehiscent capsule (or each carpel circumscissile in subfam. Penthoroideae), or a berry (subfam. Ribesioideae); seeds usually numerous, often winged; embryo small, straight with flat cotyledons, embedded in scant to copious endosperm; embryo sac of the Polygonum type, embryogeny corresponding to the Solanad or Asterad (subfam. Parnassioideae) types, or irregular after the initial stages, corresponding to no designated pattern (subfam. Ribesioideae). (Including Grossulariaceae DC., Hydrangeaceae Dumort., Iteaceae J. G. Agardh, Lepuropetalaceae Nakai, Parnassiaceae S. F. Gray, Penthoraceae Rydb. ex Britton, and Philadelphaceae D. Don.) TYPE GENUS: *Saxifraga* L.

According to the traditional Englerian interpretation, a large Rosalian family of cosmopolitan distribution comprised of about 1200 woody and herbaceous species in 80 genera; 44 species in 15 genera in the southeastern United States and about 18 additional genera in North America, primarily in the western Cordillera.

An almost impossible family to distinguish or characterize clearly because of its heterogeneity, the Saxifragaceae was divided into 15 subfamilies (17 in the 1964 edition of *Engler's Syllabus*) and numerous tribes and subtribes by Engler (1928). The subfamilies (and a number of the

tribes) exhibit a greater geographical, as well as morphological homogeneity than the family as a whole, and the family has often been divided into segregate families that generally correspond to the subfamilial (or tribal) taxa established or accommodated within the Saxifragaceae by Engler. In current systems of classification, however, there seems to be little agreement about either the circumscription or the taxonomic ranks that Engler's subfamilial taxa (particularly the woody groups) should be accorded, but, with the exception of Thorne, most investigators agree that division of the Saxifragaceae *sensu* Engler is both desirable and necessary if a more nearly natural and accessible taxonomy is to result. In view of this lack of agreement, the family is retained here provisionally in the traditional sense.

Of the 17 subfamilies recognized in the current *Syllabus*, seven (subfams. Penthoroideae, Saxifragoideae, Vahlioideae, Francoöideae, Eremosynoideae, Lepuropetaloideae, and Parnassioideae) are almost exclusively herbaceous and have vessel elements with mostly simple perforation plates. With the exceptions of subfams. Vahlioideae (*Vahlia* Thunb., in tropical and subtropical Africa, Madagascar, and India), Eremosynoideae (*Eremosyne* Endl., in Australia), and Francoöideae (two monotypic genera in South America) these herbaceous subfamilies are, for the most part, distributed in the temperate and cold-temperate regions of the Northern Hemisphere. In contrast, the ten remaining subfamilies (subfams. Ribesioideae, Baueroideae Pterostemonoideae, Hydrangeoideae, Tetracarpaeoideae, Iteoideae, Brexioideae, Escallonioideae, Montinioideae, and Phyllonomoideae) are predominantly woody taxa with vessel elements with mostly scalariform perforation plates, and, with the exception of the Ribesioideae and the major part of the Hydrangeoideae that have disrupted Arcto-Tertiary distributions in the Northern Hemisphere, these subfamilies are mostly confined to the Southern Hemisphere and tropical and subtropical regions.

The greatest number of genera (ca. 30) occurs in North America, where genera in nine subfamilies (two restricted to Mexico: Phyllonomoideae [*Phyllonoma* Willd.] and Pterostemonoideae [*Pterostemon* Schauer]) are represented. The Saxifragoideae and, to a lesser extent, the Hydrangeoideae are particularly well represented, especially in the western Cordillera, an area of diversification within subtribe Saxifragineae (ca. 17 genera) and tribe Philadelpheae (five or six genera) of the Hydrangeoideae.

Savile (1954, 1961), in studies of the taxonomy of a group of microcyclic rusts of the genus *Puccinia* that occur on species of several genera of the Saxifragineae (including *Mitella, Tiarella, Bergenia, Saxifraga, Chrysosplenium, Heuchera, Tolmiea,* and *Tellima*), has gained indirect insights concerning the saxifragaceous hosts. He has concluded on the basis of observed evolutionary trends in the morphology of the rusts that they are "mostly of a single evolutionary group" that probably originated in the Himalayan region and there parasitized an underived saxifragaceous host-complex. The underived saxifragaceous complex probably crossed the Bering land bridge several times in the late Tertiary and Pleistocene times.

and radiated into new niches in the western Cordillera. Migrations probably occurred in the opposite direction after the initial North American radiation, and Savile has suggested that the oldest species of *Mitella* and *Tiarella* (both genera with eastern North American, western North American, and Asian species), and the oldest species of *Heuchera* and *Saxifraga* are roughly the same age. Differentiation among genera in North America has been primarily in adaptation to differing ecological situations and the characters that define genera include specialized adaptations for pollination and dispersal. Generic limits of a number of genera are open to dispute, but study of floral mechanisms and breeding systems will undoubtedly aid in their resolution.

In the Englerian sense, the family is not only heterogeneous morphologically, encompassing annual, biennial, and perennial herbs, shrubs, trees, and woody vines of essentially every ecological situation, but it also exhibits considerable anatomical, palynological, chemical, cytological, and embryological diversifications. The full range of this diversity is too great to discuss here, but information pertinent to the genera occurring in our area is included in the generic discussions.

Except for various species that are cultivated in rock gardens and perennial borders and some of the woody genera that are of considerable ornamental value, the Saxifragaceae are of little economic importance. Currants and gooseberries (*Ribes*) are cultivated commercially only on a relatively small scale.

KEY TO THE GENERA OF SAXIFRAGACEAE IN THE SOUTHEASTERN UNITED STATES

General characters: *Sensu* ENGLER, *a poorly defined family of annual, rarely biennial, or perennial herbs, shrubs, woody climbers, or trees; flowers with the number of stamens mostly definite, carpels same number or commonly fewer than sepals and either free or partially to completely connate; sepals rarely free (insertion hypogynous), usually connate at least at base, forming a floral cup adnate to ovary; insertion of corolla and androecium perigynous to epigynous on inner surface of floral cup; ovules anatropous; fruits capsules or sometimes berries; seeds usually small, sometimes winged. Generally distinguished from Rosaceae by seeds with copious endosperm, opposite as well as alternate, mostly exstipulate leaves, and usually fewer carpels and stamens; distinguished from Crassulaceae by carpels not subtended by glands and floral parts of a less regular numerical pattern.*

A. Plants herbaceous.

B. Staminodia absent; styles not commissural; fruit a septicidal or circumscissile capsule or dehiscing apically between styles.

C. Carpels 5–7; fruit a 5–7-beaked capsule, each carpel circumscissile (subfam. Penthoroideae). . . . . 1. *Penthorum.*

C. Carpels 2 or 3; fruit a septicidal capsule or dehiscing between styles (subfam. Saxifragoideae).

D. Leaves ternately decompound; flowers imperfect; plants polygamodioecious. . . . . 2. *Astilbe.*

D. Leaves simple; flowers perfect; plants monoecious.

E. Corolla present; flowers in racemes or panicles.
F. Petals pinnatifid or fimbriate; flowers in simple racemes; cauline leaves subopposite. .... 3. *Mitella.*
F. Petals not pinnatifid or fimbriate; cauline leaves (if present) alternate.
G. Ovary 1-loculate; placentae parietal.
H. Inflorescence racemose; stamens 10; carpels unequal. ..... 4. *Tiarella.*
H. Inflorescence paniculate; stamens 5; carpels equal. ..... 5. *Heuchera.*
G. Ovary 2-loculate (at least above); placentae axile.
I. Leaves palmately lobed; stamens 5. ..... 6. *Boykinia.*
I. Leaves not palmately lobed; stamens 10. ..... 7. *Saxifraga.*
E. Corolla absent; flowers solitary in leaf axils or in leafy cymes. ..... 8. *Chrysosplenium.*

B. Staminodia present; styles commissural; fruit a loculicidal capsule (subfam. Parnassioideae).
J. Plant a diminutive winter annual to 2 cm. tall; both basal and cauline leaves present. ..... 9. *Lepuropetalon.*
J. Plants perennial from rhizomes or caudices; leaves all basal. .... 10. *Parnassia.*

A. Plants shrubs or woody vines.
K. Leaves alternate or clustered on short, alternate spur branches.
L. Leaves palmately lobed; ovary inferior; fruit a berry (subfam. Ribesioideae). ..... 11. *Ribes.*
L. Leaves entire; ovary superior; fruit a capsule (subfam. Iteoideae). ..... 12. *Itea.*

K. Leaves opposite, sometimes whorled with 3 at a node (subfam. Hydrangeoideae).
M. Petals usually 4; stamens 20–40; fruit an unribbed woody capsule, dehiscing longitudinally. ..... 13. *Philadelphus.*
M. Petals 5 or 8–12; fruit a strongly ribbed capsule, dehiscing either apically or between the capsule ribs.
N. Stigmas 2 or 3, free; fruit dehiscing apically between the styles; nonclimbing shrubs. ..... 14. *Hydrangea.*
N. Stigmas capitate, with radiating stigmatic lines; fruit dehiscing between capsule ribs; woody vines climbing by roots. ..... 15. *Decumaria.*

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Subfam. PENTHOROIDEAE Engler

1. **Penthorum** Linnaeus, Sp. Pl. 1: 432. 1753; Gen. Pl. ed. 5. 197. 1754.

Erect, fibrous-rooted, often semiaquatic perennial herbs up to 10 dm. tall, multiplying, spreading, and perennating by horizontal stolons or rhizomes. Stems terete, glabrous, and often decumbent below, angled, finely pubescent, and usually widely branched above. Leaves bright green and shining, alternate, and short petiolate; blades thin, elliptic with an attenuate or narrowly cuneate base, an acuminate apex, and serrulate margins; venation pinnate with a prominent midvein. Flowers perfect, arranged in secund, scorpioid [or corymb-like], terminal and axillary cymes. Calyx of 5 (6–7) sepals, united below, forming a shallow, saucer-shaped floral cup; calyx lobes free above, ovate with irregularly toothed margins and acute apices, erect during anthesis, becoming reflexed in fruit, persistent. Corolla absent or comprised of 1–7 greenish [or white], lanceolate, slightly clawed petals inserted on the rim of the floral cup, usually shorter than the calyx lobes. Stamens 10, inserted on the edge of the floral cup; filaments terete, tapering only slightly to the basifixed, 2-loculate, longitudinally dehiscent, oblong anthers; pollen subprolate, 3-colporoidate, the sexine as thick as the nexine. Gynoecium 5–7 (typically 5 or 6) carpellate, syncarpous and adnate to the floral cup below the placental area; styles erect during anthesis, terminated by slightly rounded, capitate stigmas; each carpel with many crassinucellar, bitegmic, anatropous ovules on a well developed, pendulous, marginal placenta on the adaxial suture above the syncarpous region. Carpels becoming obliquely oriented in fruit, producing a 5–7 beaked, reddish capsule, the beak of each carpel circumscissile above the syncarpous region of the gynoecium. Seeds many, small, ellipsoid to obovoid, the surface tuberculate to echinate; embryo large, straight; endosperm of the *ab initio* Cellular type, scanty. Base chromosome numbers 8, 9. TYPE SPECIES: *P. sedoides* L. (Name from Greek, *pente*, five, and *horos*, a mark, from the characteristically 5-merous plan of the flower.) — DITCH-STONECROP.

Two species, *Penthorum sedoides*, $2n = 18$, in eastern North America, and *P. chinense* Pursh, $2n = 16$, in eastern Asia, ranging from eastern Siberia and Manchuria through Korea, Japan, and China. *Penthorum sedoides* grows in the wet, muddy soils of river flood plains, in swamps and low woodlands, along ditches, and in fallow fields from New Brunswick, Maine, and Quebec southward through Florida and westward to southern Ontario, Minnesota, Nebraska, Kansas, Oklahoma, and eastern Texas.

FIGURE 1. **Penthorum.** a–g, *P. sedoides*: a, tip of flowering shoot showing scorpioid cymes, × 1/2; b, flower with five-carpellate gynoecium, × 8; c, vertical section of flower, showing pendulous, marginal placenta on adaxial suture of one carpel above the syncarpous region, × 8; d, fruit, beginning to dehisce, × 4; e, fruit showing circumscissile stylar beaks of several carpels, × 5; f, seed, × 50; g, perennating horizontal rhizome, × 3/4.

Although less frequently encountered in the mountains of our region, *P. sedoides* occurs in every physiographic province and probably in every Coastal Plain county. Originally considered conspecific with *P. sedoides*, *P. chinense* differs from the American species in its lower chromosome number, its narrower leaves, shorter and thicker styles, and its fewer-flowered, corymb-like inflorescences. Additional species, *P. intermedium* Turcz. and *P. humile* Regel, attributed to the genus from Asia are probably based on plants that are variants of *P. chinense*.

Vegetative and floral variation is considerable in both species of *Penthorum*, and insect damage to the thin, shining leaves gives the plants a weedy aspect. Greatest vegetative differences seem to occur in populations that are subject to periodic inundation and alternating periods of drought; during wet seasons the plants may be semi-aquatic. Differences in the number of carpels, sepals, and petals, however, do not appear to be correlated with habitat, and great variability is often evident within the flowers of a single inflorescence.

Flowering occurs more or less continuously throughout the summer months and until frost, and a great number of small seeds are produced

within each carpel of the flower. Vegetative reproduction and perennation of the plants are accomplished by horizontal stolons or rhizomes that are produced from the rootstock towards the end of the growing season (see FIG. 1, g). Rhizome initiation appears to be triggered by shortening day length.

Morphologically well marked from other saxifragaceous genera by its reddish capsules with five to seven circumscissile carpels, *Penthorum* has not always been included within the Saxifragaceae. Alternatively placed in its own monogeneric family, the Penthoraceae Rydb. ex Britton, or included in the Crassulaceae, the floral structure of *Penthorum* seems to be intermediate between the Crassulaceae and Saxifragaceae. The union of the sepals into a shallow floral cup and the basally syncarpous gynoecium (not subtended by a gland) ally the genus to the Saxifragaceae, whereas the number of floral parts suggests affinities within the Crassulaceae. The obviously crassulaceous genera *Diamorpha* Nutt. and *Triactinia* Hook. f. & Thoms. exhibit shallow floral cups and syncarpous gynoecia, and De Candolle (1828) placed *Penthorum* and *Diamorpha* in the tribe Crassulaceae Anomalae. Torrey & Gray (1840) also grouped these two genera as the tribe Diamorpheae in the Crassulaceae, but Baillon (1871) removed *Penthorum* to a monotypic tribe in the Saxifragaceae, Berger (1928) omitted *Penthorum* from his treatment of the Crassulaceae, and Engler (1928) included the genus in a monotypic subfamily in the Saxifragaceae that he considered to be the least derived in the family.

On the basis of floral morphology, Quimby (1971) has given indirect support to the inclusion of *Penthorum* in the Saxifragaceae, inasmuch as he concluded that the Crassulaceae is a natural group if *Penthorum* is excluded. From embryological evidence, Mauritzon (1933, 1939) claimed strong reinforcement for placement of *Penthorum* in the Saxifragaceae, and Jay (1971) concluded from chemical data that *Penthorum* is significantly different from the Crassulaceae but very similar to *Bergenia* and *Peltoboykinia* in the Saxifragoideae. Cronquist, while admitting that the placement of *Penthorum* is largely a matter of opinion, has included the genus in the Saxifragaceae, while Takhtajan (1959) has chosen to recognize the Penthoraceae and has noted the exclusively scalariform perforation plates of the vessels in these herbs as a diagnostic family character.

Penthorum is occasionally a noxious weed that may compete with crop plants or foul irrigation ditches. Local medicinal usages of *Penthorum* include its use as a demulcent, astringent, and laxative.

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Subfamily SAXIFRAGOIDEAE A. Br.

Tribe SAXIFRAGEAE DC.

Subtribe **Astilbinae** Engler

2. **Astilbe** Buch.-Ham. in D. Don, Prodr. Fl. Nepal. 210. 1825.

Robust [or delicate], sometimes branched perennial herbs up to 2 m. high from stout rhizomes. Basal and cauline leaves similar, alternate, long petiolate, the petioles with scarious stipules at their bases; leaf blades [rarely simple and leaves all basal] ternately decompound, irregularly odd-bipinnate or odd-tripinnate, the leaflets on short petiolules or subsessile, ovate to elliptic in outline and often irregularly 1–3(5)-cleft or lobed; leaflet margins coarsely and irregularly double serrate or crenate, the teeth and lobes with mucronate tips; bases of leaflets oblique, truncate, or cordate, the apices acuminate; venation pinnately netted. Inflorescence a widely spreading, many-branched, plume-like [or congested and spike-like], terminal bracteate panicle, the flowers short pedicellate, becoming reflexed in fruit, perfect or imperfect (in ours, the flowers either perfect, appearing perfect but apparently functionally staminate, or carpellate and the plants appearing to be hermaphroditic, polygamous, or functionally polygamodioecious). Calyx of 5(7–10) deltoid sepals, connate at the base, forming a shallow campanulate to obconic floral cup with 5(7–10) short, erect, imbricate and persistent calyx lobes. Corolla absent [or consistently present] or variously of 1–5 erect, white, yellowish [pink, red, or purplish], spatulate to subulate petals inserted on the inner surface of the floral cup. Androecium abortive in imperfect flowers; when developed, obdiplostemonous, the [5, 8, or] 10 stamens erect, about twice as long as and inserted at the base of the floral cup, the filaments tapering gradually to the basifixed, cordate-orbicular, tetrasporangiate anthers; anthers white or yellowish; pollen grains 3-colporoidate. Gynoecium 2(rarely 3)-carpellate, the carpels connate below, tapering into two free styles and terminated by capitate stigmas; ovary superior with a poorly differentiated disc at the

base, 2-loculate, with numerous anatropous, crassinucellar, bitegmic ovules on axile placentae in the connate region. Fruit a 2-beaked capsule composed of the two follicle-like carpels, each dehiscing longitudinally in the stylar region. Seeds numerous, oblong-cylindrical, the lustrous, reddish-brown seed coat winged and often twisted at both ends; embryo small, straight, embedded in endosperm of the *ab initio* Cellular type; embryo sac of the Polygonum type. Base chromosome number 7. (*Hoteia* Morr. & Decne.) TYPE SPECIES: *A. rivularis* Buch.-Ham. (Name from Greek, *a*, without or lacking, and *stilbe*, brilliance or sheen, in reference to the foliage of *A. rivularis* in contrast to that of *Aruncus* (Rosaceae), which it resembles.) — FALSE GOATSBEARD, FEATHER-TREES.

A well-defined genus with one or perhaps two species endemic to the southern Appalachians in North America and about 23 in eastern Asia from Japan through China into the Himalayan region and extending southward into New Guinea. *Astilbe biternata* (Vent.) Britt. (*Tiarella biternata* Vent., *A. decandra* D. Don), $2n = 28$, an upright, sometimes branched herb up to one or two meters high with glandular trichomes and large, compound leaves is restricted to the Appalachian Mountains from Mingo County, West Virginia southward through Virginia and Kentucky, to the Carolinas, Tennessee, and northwestern Georgia. A second species, *A. crenatiloba* (Britt.) Small (*A. decandra* var. *crenatiloba* Britt., *A. biternata* var. *crenatiloba* (Britt.) Wheel.), has been recognized from the slopes of Roan Mountain on the North Carolina-Tennessee boundary, but this taxon is probably only a local variant of *A. biternata* with crenately lobed leaflets.

Growing in rich woods and on moist, shaded or sometimes open seepage slopes, *Astilbe biternata* is often confused with *Aruncus dioicus* (Walt.) Fern. (Rosaceae), and this species pair, as well as Asiatic species of both genera, are striking examples of convergent evolution. Occupying the same or similar habitats as *Astilbe biternata*, *Aruncus dioicus* is more widely distributed in eastern North America, occurring on the Piedmont and in the mountains from Pennsylvania southward through the Carolinas and into northern Georgia and Alabama and westward into Arkansas, Missouri, and Iowa. *Aruncus dioicus* can easily be separated from *Astilbe biternata*, however, by its simple trichomes, 15 or more stamens in staminate flowers, and/or its three or four carpels in carpellate flowers.

In carpellate flowers of *Astilbe biternata* the androecium is abortive, and plants with apparently perfect flowers are probably functionally staminate inasmuch as the carpels are relatively undeveloped and the stigmas appear to be undifferentiated and unreceptive. Although experiments have not been conducted and despite occasional fruit set in inflorescences of perfect flowers, *A. biternata* seems to be largely dioecious. Anthesis occurs from May into August, and pollination is undoubtedly by insects. The fruits mature during the late summer and fall, and the numerous small seeds are probably scattered from the dehisced capsules by wind and passing animals.

Engler (1928) divided the genus into sect. ASTILBE (sect. *Compositae*

Engl.), which is composed of species with compound leaves, and sect. SIMPLICIFOLIAE, which includes only one or two species with simple leaves of the Himalayan region. Within sect. ASTILBE, *A. biternata* appears to be intermediate between a group of apetalous species and other species with flowers that consistently have well developed corollas. Flowers of some plants of *A. biternata* are apetalous, while in other plants the flowers have corollas, although there is considerable variation in the number, size, and shape of the petals.

Hamel (1953) hypothesized that the variable corolla trait in *Astilbe biternata* might have a chromosomal and genetic basis that reflects the species' origin. Both diploid, $2n = 14$, and tetraploid, $2n = 28$, chromosome numbers are recorded for the genus, and Hamel proposed on the basis of the corolla trait, chromosome numbers, and chromosome idiograms, that *A. biternata*, a tetraploid with $2n = 28$, may be an amphidiploid of hybrid origin between petalous and apetalous species. Interspecific hybridization has not been detected or necessarily suspected in nature, but numerous fertile hybrids and trihybrids have been produced between species under cultivation. The apparent ease with which garden hybrids have been made suggests that barriers to gene flow between species in nature are probably largely geographical and/or ecological.

Astilbe was aligned by Engler with *Rodgersia* A. Gray, $2n = 30, 36, 60$, an eastern Asiatic genus of six species characterized by perfect flowers and palmately compound leaves with scarious stipules, and the monotypic *Astilboides* Engler, $2n = 34$, ca. 36, which was segregated from *Rodgersia* primarily because of its peltate leaves. Together, these three genera comprise subtribe Astilbinae Engler within the tribe Saxifrageae of subfam. Saxifragoideae, although it has been suggested that the morphological similarities between these genera may be due to evolutionary convergence. Jay (1971) has concluded tentatively on the basis of chemical evidence that while *Astilbe* and *Rodgersia* seem to be allied, *Astilboides* is chemically distinct and probably has greater affinities elsewhere in the Saxifragoideae. Dandy (1927) asserted that *Astilbe* is most closely allied to *Tanakaea* Franchet & Savat., a Chinese and Japanese genus of one or two species with apetalous, imperfect flowers included in subtribe Leptarrhenineae by Engler (1928).

A number of the Asian species are used as garden ornamentals. The numerous garden hybrids (involving *Astilbe japonica* (Morr. & Decne.) A. Gray, *A. astilboides* Lemoine, *A. Thunbergii* (Sieb. & Zucc.) Miq., and *A. Davidii* (Franchet) Henry) were mostly developed by Lemoine, in France, and by Arends, in Germany. In the Philippine Islands the Ingorots dried leaves of *A. philippensis* Henry for smoking, but other uses of *Astilbe* have not been reported.

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Subtribe **Saxifraginae** Engler

3. **Mitella** Linnaeus, Sp. Pl. 1: 406. 1753; Gen. Pl. ed. 5. 190. 1754.

Low, pubescent perennial herbs from scaly, creeping rhizomes [often producing leafy stolons toward the end of the growing season]. Basal leaves alternate from the rhizome and long petiolate; leaf blades 3–5(–7)-lobed [or entire; orbicular, reniform, or], broadly ovate in outline with a cordate base; margins crenate with mucronate lobes; venation palmate; petioles slender, dilated at the stipulate base, the stipules inconspicuous, basally adnate to the petiole, membranaceous above with acute apices. Cauline leaves 2, 3 [or 0], subopposite to opposite or alternate, subsessile or distinctly petiolate. Flowers perfect, short [to long] pedicellate and well spaced in elongate [several to] many-flowered simple racemes that become ± secund in fruit; rachis of raceme and pedicels finely glandular pubescent, each pedicel subtended by a small, entire [pinnatifid, or fimbriate] membranaceous bract. Sepals 5, persistent and united below, forming an oblong patelliform [campanulate, or turbinate] floral cup, the calyx lobes erect or slightly recurved at the acute apices [or the sepals connate at the base and forming a strongly flattened floral cup with the calyx lobes strongly reflexed]; floral cup with a ring of glandular tissue on the inner surface below the insertion of the anthers. Corolla white [greenish-yellow, or purple], of 5 [or 0], early deciduous petals inserted on [or just below] the rim of the floral cup, sessile or slightly clawed, the blade pinnately

FIGURE 2. **Mitella.** a–j, *M. diphylla*: a, flowering plant, showing simple racemose inflorescences and paired, opposite cauline leaves, × 1/2; b, detail of raceme with bracts subtending flowers, × 3; c, flower showing collar of glandular tissue on inner surface of floral cup beneath insertion of anthers, × 10; d, longitudinal section through flower, showing glandular collar and parietal placenta, × 12; e, detail of dehisced anther, × 25; f, immature capsule after corolla disarticulation, × 6; g, top view of immature capsule showing line of dehiscence between styles, × 6; h, transverse section through floral cup and capsule, × 6; i, erect "splash-cup" capsule after dehiscence, × 6; j, seed, × 12.

cleft [pectinate-pinnatifid with the segments held at right angles, or rarely entire]. Androecium obdiplostemonous, of 10 stamens [or (4) 5, and either opposite or alternate with the calyx lobes (when 4, one stamen modified as a staminodium)]; anthers yellow, oblong [or cordate to reniform], longitudinally dehiscent. Gynoecium 2-carpellate, the styles free, short and thick with crescent-shaped stigmas [or capitate and 2–4-lobed, or the styles slender and tapering to small, pointed stigmas]; ovary 1-loculate, superior [to half-inferior], the basal portion adnate to the floral cup; several [or numerous] crassinucellar, bitegmic ovules oriented on 2 parietal placentae on the sutures between the 2 carpels. Fruit a 2-beaked capsule, dehiscing between the styles along lines above the placentae; seeds

several [to numerous], narrowly ovoid, black and shining, the surface pustulate to tuberculate [or smooth], endosperm usually copious, of the Helobial [or *ab initio* Cellular] type. Base chromosome number 7. (Including *Mitellastra* (Torrey & Gray) Howell, *Ozomelis* Raf., *Pectiantia* Raf., *Drummondia* DC. non W. J. Hooker, and *Mitellopsis* Meisner.) LECTOTYPE SPECIES: *M. diphylla* L.; see P. A. Rydberg, N. Am. Fl. 22: 91. 1905. (Name a diminutive of Latin, *mitra*, a cap or turban, an allusion to the miter-like appearance of the flowers and undehisced capsules.) — MITREWORT, BISHOP'S-CAP.

A vegetatively homogeneous genus (leaves stipulate, basal) of about 20 species with centers of diversity in the Cordillera of western North America and eastern Asia; *Mitella diphylla* L. in our region, seven or eight species elsewhere in North America, eleven in Japan, one in Taiwan, and one widespread species ranging from Labrador to Central Asia.

Species of *Mitella* with the calyx forming a campanulate to oblong-patelliform floral cup, oblong anthers, capitate or crescent-shaped stigmas, and a white or purple-tinged corolla of pinnately-cleft petals belong to sect. MITELLA (subgen. *Eumitella* Torrey & Gray *pro parte*, sect. *Eumitella* (Torrey & Gray) Rosendahl, subgen. *Spuriomitella* Boissieu, subgen. *Pectinella* Boissieu *pro parte*). Primarily North American, this section includes *M. diphylla* L., $2n = 14$, a species of the eastern deciduous forest; the closely allied *M. stauropetala* Piper, *M. trifida* Graham, and *M. diversifolia* Green, of the western Cordillera; and *M. integripetala* Boissieu and the apetalous *M. doiana* Ohwi, both of Japan. In our area, *M. diphylla*, found on moist wooded bluffs, rocky slopes, and stream banks and usually colonial, is readily distinguished by its elongate racemes of small, inconspicuous and delicate flowers and its stratified foliage. The two subopposite cauline leaves are usually held horizontally about halfway up the flowering stem above the basal leaves, giving the plants a distinctive appearance. Recognized variants from the typical form include f. *triphylla* Rosendahl (three alternate cauline leaves) and f. *oppositifolia* Rosendahl (paired leaves opposite). Restricted to the mountains of northwestern Georgia, western North Carolina, and eastern Tennessee in our area, *M. diphylla* ranges northward into New Hampshire, Vermont, and Quebec, and westward to Ontario, central Minnesota, and eastern Missouri.

Section MITELLASTRA (Torrey & Gray) Walpers (subgen. *Mitellastra* (Meisner) Torrey & Gray, subgen. *Mitellina* Torrey & Gray, subgen. *Pectinella* H. Boiss. *pro parte*) includes those species with the calyx forming a strongly flattened, saucer-shaped floral cup, cordate to reniform anthers, a greenish-yellow or purple corolla of pectinate-pinnatifid petals with the divisions spreading nearly at right angles, and pointed or strongly 2–4-lobed stigmas. *Mitella caulescens* Nutt., $2n = 14$, *M. pentandra* Hook., $2n = 14$, *M. Breweri* A. Gray, $2n = 14$, and *M. ovalis* Greene are endemic to the Cordillera of western North America, while ten additional species of the section are indigenous to Japan. *Mitella japonica* (Sieb. & Zucc.) Maxim., $2n = 14$, a variable species with several varieties, is also

known from Taiwan. *Mitella nuda* L., $2n = 28$, a wide-ranging species of the Boreal belt, is known from Central Asia to Labrador. Its amphi-Pacific distribution links the southern cordilleran centers of diversity in Japan and North America and overlaps the range of *M. diphylla* in northeastern North America. A species of cool, coniferous forests and mossy swamps and bogs, *M. nuda* is usually ecologically isolated from *M. diphylla*, although putative hybrids from Wisconsin have been recognized as *M.* × *intermedia* Bruhin ex Rydb. pro sp. (*M. diphylla* f. *intermedia* (Bruhin) Rosend.).

Vegetative differences between species of *Mitella* consist primarily of slight differences in leaf morphology; the presence or absence, number, and positioning of cauline leaves; and the numbers of flowers comprising the simple racemes. Specific and subgeneric categories in *Mitella* have been based primarily on floral characters, and historically the species have been placed in several genera on the basis of stamen number and position as well as differences of ovary-floral-cup relationships. The trend toward a broad circumscription of the genus was initiated by Hooker, and Torrey & Gray (1840) united the several previously recognized segregate genera under four subgenera. De Boissieu (1899) recognized two subgenera and three sections, whereas Rydberg (1905), reverting to the narrow generic and specific concepts of Rafinesque, Meisner, and Howell, placed 18 North American species in four genera. Rosendahl (1914), however, redefined subgeneric categories and regrouped the species in two sections under *Mitella*. Despite differences in stamen number and position between species within a section, Rosendahl's division appears to be a natural one, reflecting two lines of floral evolution in a genus adapted to moist humid forests.

Intergeneric hybrids involving *Mitella diphylla*, *M. nuda*, and *Tiarella cordifolia* L., $2n = 14$, have also been detected on grounds of intermediate morphology. *Mitella* × *tiarelloides* Engler, from New Brunswick, is a postulated hybrid between *M. nuda* and *T. cordifolia*, while *M.* × *Grayana* Engler combines characters of *M. diphylla* and *T. cordifolia*. The putative hybrids are apparently sterile, and at least in hybrids involving *M. nuda*, sterility may be due to triploidy.

Although reported to be characterized by proterogyny, flowers of *Mitella diphylla* appear to be slightly proterandrous. Exhibiting no stamen movements, the flowers are adapted to pollination by small, probing insects. Syrphid flies and short-tongued bees are the most frequent visitors, and as they move over the flowers in search of nectar (produced by a collar of glandular tissue on the inner surface of the floral cup) they collect pollen on their mouth parts. Nectar secretion apparently is ephemeral, since once the stigmas become receptive and the ovary begins to enlarge, the glandular collar becomes shriveled and obscured.

During anthesis, flower orientation in the raceme is rather variable, but as the fruits mature the racemes become decidedly secund, and the capsules become erect on their short pedicels. Dehiscence of the capsules along lines between the styles but above the two parietal placentae exposes the several to numerous seeds and creates a shallow, cup-shaped fruit with a flared,

two-beaked rim. As in *Chrysosplenium*, the seeds are bounced from the "splash-cup" when drops of water land in the upright capsule.

The base chromosome number of the genus is seven, and, with the exception of *Mitella nuda*, a tetraploid with $2n = 28$, all investigated species are diploids. Embryological studies have revealed variation in the mode of endosperm formation. In *M. diphylla*, endosperm formation corresponds to the Helobial pattern of development, whereas in *M. pentandra* formation follows the *ab initio* Cellular sequence, and a nonaggresive haustorium comprised of four cells is formed in the chalazal chamber.

Similar vegetative morphology, inflorescence structure, base chromosome numbers, and chemistry unite *Mitella* with *Tiarella* L. ($x = 7$), *Heuchera* L. ($x = 7$), *Tolmiea* Torrey & Gray ($x = 7$), *Bensoniella* Morton (*Bensonia* Abrams & Bacig.), *Tellima* R. Br. ($x = 7$), *Conimitella* Rydberg, and *Elmera* Rydberg in an apparently natural group within the Saxifragoideae characterized by two-carpellate, one-loculate gynoecia with parietal placentae. Only *Mitella* and *Tiarella* have Asian species, and with the exception of these two genera and *Heuchera*, the remaining are monotypic and endemic to the Cordillera of western North America. Savile (1954, 1961) has suggested that the genera of this assemblage have become segregated from one another through adaptations to differing ecological conditions. "They are accordingly largely distinguished [from one another] by seed-dispersal mechanisms or pollination mechanisms, which may mask relationships or suggest them in convergent forms." (Savile, 1961, pp. 171, 172.) Continued cytological studies and hybridization experiments, as well as the application of other techniques will undoubtedly be of value in further elucidating generic relationships and may result in redefined generic concepts.

None of the species of *Mitella* has reported economic value, although the plants are powerful astringents, and the roots of *M. pentandra* have been reported as effective antidotes for diarrhea.

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4. **Tiarella** Linnaeus, Sp. Pl. 1: 405. 1753; Gen. Pl. ed. 5. 190. 1754.

Low, often evergreen, pubescent perennial herbs from scaly, creeping rhizomes, some producing leafy stolons. Basal leaves alternate from the rhizome and long petiolate; leaves simple [or trifoliolate], the blade palmately veined, cordate or broadly ovate in outline and usually palmately 3–7-lobed [or cleft], the margins dentate or crenate with broad, mucronate lobes; petioles dilated at the stipulate base, the stipules adnate to the petioles below, membranaceous above, tapering to acute or acuminate apices. Scapes naked or with 1–3 alternate, short-petiolate cauline leaves, like the basal leaves. Flowers perfect, short-pedicellate, in simple racemes, occasionally with paniculate branches at the base [or the inflorescence a panicle]; each pedicel subtended by a delicate, filiformly dissected bract. Sepals 5, imbricate in bud and connate at the base, forming a shallow, regular [or slightly irregular] floral cup, the calyx lobes spreading at anthesis, becoming reflexed in fruit. Corolla white or purplish-tinged, regular [or somewhat irregular], of 5 clawed, early deciduous petals exceeding [or slightly shorter than] the calyx lobes, inserted on the rim of the floral cup, the blades elliptical to oblanceolate [linear or subulate], the apices attenuate or often 3-toothed. Stamens 10, equal [or stamens opposite sepals longer than stamens opposite petals]; filaments persistent, slender and often clavate; anthers oval [or oblong], yellow or orange, dehiscing longitudinally. Gynoecium 2-carpellate, the carpels united below, forming a 1-loculate, superior ovary with 2 parietal placentae; ovules several to numerous, crassinucellar, and bitegmic; the carpels free above, unequal, and incompletely sealed along their adaxial sutures above the placentae, with the shorter of the two sometimes appressed and partially inclosed within the longer, the short styles (or only one of the two) terminated by inconspicuous, capitate stigmas. Fruit a 2-winged, valvate capsule, dehiscing between the free upper portions of the carpels, the expanded, membranaceous lamina of the carpels forming two unequal

FIGURE 3. **Tiarella.** a–f, *T. Wherryi*: a, flowering and fruiting plant, × 1/4; b, detail of raceme, × 1/2; c, flower, showing clavate anthers and superior ovary, × 5; d, longitudinal section of gynoecium showing parietal placenta, partially open lower carpel, and absence of stigma on upper carpel, × 8; e, mature fruit showing unequal open carpels, × 3; f, seed, × 16. g, *T. cordifolia*: gynoecium, illustrating stigmas and incompletely sealed sutures on both carpels, × 5.

(sometimes subequal) wings. Seeds several, ovoid with a truncate base, the surface puncticulate, black and shining; embryo straight. Base chromosome number 7. (Including *Petalosteira* Raf. and *Blondia* Necker ex Raf.) LECTOTYPE SPECIES: *T. cordifolia* L.; see P. A. Rydberg, N. Am. Fl. 22: 117. 1905. (Name a diminutive of Greek, *tiara*, a high headdress, in allusion to the appearance of the capsules.) — FALSE MITREWORT, FOAMFLOWER.

A small genus of six, seven, or perhaps as few as three species adapted to cool, moist forests of mountainous and coastal regions of North America (variously one to four in Pacific Northwestern America, one or two in eastern North America), and one in eastern Asia (*Tiarella polyphylla*). Distinguished from allied genera of the Saxifragoideae by its gynoecium of two unequal and incompletely sealed carpels, the genus in North America has been divided into two geographical subgenera. The eastern American species comprise subgenus TIARELLA (subgen. *Eutiarella* Torrey & Gray), distinguished by simple racemose inflorescences, regular flowers with clawed petals, equal stamens, and anthers that are wider than long after dehiscence. The western American species, all included in subgen.

ANTHONEMA Nuttall ex Torrey & Gray, are characterized by paniculate inflorescences of somewhat irregular flowers with subulate petals, stamens of two lengths, and anthers longer than wide after dehiscence. This division of the genus appears less tenable, however, if the single Asian species, *T. polyphylla* D. Don, $2n = 14$, ranging from the eastern Himalayas through western and central China to Taiwan and Japan, is grouped with American species. The flowers of *T. polyphylla* are regular, but the petals are subulate to linear (or rarely lacking); the stamens are of one length, but anther dimensions are variable after dehiscence. In addition, like some forms of eastern American *Tiarella*, its racemes often have short paniculate branches at the base.

In the southeastern United States, two species of *Tiarella*[2] have been recognized, although specific lines have aroused controversy. *Tiarella Wherryi* Lakela, based on plants from southwestern North Carolina, Tennessee, and Alabama, was segregated from the wide-ranging northern and stoloniferous *T. cordifolia* L., $2n = 14$, because of floral differences and a nonstoloniferous habit, yet some workers have maintained that *T. cordifolia* consists of both stoloniferous and nonstoloniferous forms.[3] Wherry (1940, 1949), while upholding *T. Wherryi* on the strength of floral and foliar characters, as well as a difference in blooming period, recognized nonstoloniferous forms from the Blue Ridge and Piedmont of Virginia and North Carolina as *T. cordifolia* var. *collina* Wherry. Fernald (1943), however, included all nonstoloniferous southeastern tiarellas in *T. Wherryi* and correlated the lack of stolons with a modified and less variable group of floral and inflorescence characters. Radford, Ahles, & Bell (1968), on the other hand, include all nonstoloniferous forms in *T. cordifolia* var. *collina* Wherry.

In addition to the lack of stolons, *Tiarella Wherryi* differs from *T. cordifolia* in its relatively broad and short capsule valves or wings with rounded tips, its tapering staminal filaments after anther disarticulation, and its sometimes purplish-tinged flowers with the lower pedicels 6–10 mm. long. In *T. cordifolia* the capsule wings are elongate and relatively narrow, terminating in a subacuminate tip, the staminal filaments have a blunt apex, the flowers are usually white, and the lower pedicels are 7–13 mm. long. The shorter of the two carpels in flowers of *T. Wherryi* lacks the small, capitate stigma present on both carpels in flowers of *T. cordifolia*.

Widespread from Nova Scotia and New Brunswick to Ontario and southward through the Appalachian Mountain states, *Tiarella cordifolia* reaches the southern limits of its range in the mountains of North and South Carolina, Tennessee, and Georgia. Occupying moist, forested slopes and woodland margins, the species ranges westward through West Virginia

[2] A third species, *Tiarella macrophylla*, was described by Small (Fl. Southeast. U.S. 501. 1903) from Tryon Mountain, North Carolina. The type specimen, however, consists of basal leaves of *Heuchera villosa* Michx. and racemes of *T. cordifolia* (cf. Lakela, 1936).

[3] Cf. Wherry (1940) for information on the Linnaean description of *T. cordifolia* and the materials on which it was based. This problem needs further clarification.

and Pennsylvania to Ohio and Michigan and is known from a disjunct population in Wisconsin. *Tiarella Wherryi* is primarily a species of the Piedmont where it replaces *T. cordifolia*, but it also occupies habitats similar to those of *T. cordifolia* in the mountains of the Southeastern States. It has been impossible to determine from herbarium specimen labels, however, whether the two species occur in mixed populations or if they are restricted to different altitudinal zones in the mountains. On the Piedmont, *T. Wherryi* is known from scattered localities in Mississippi, Alabama, and Georgia, but the species is most frequently encountered in the Carolinas and Virginia.

Problems encountered in the taxonomic treatment of southeastern tiarellas are undoubtedly partially due to variation within *Tiarella cordifolia* sensu stricto, but are also related to lack of care in including stolons, when present, with pressed herbarium specimens. Attempts to delimit subspecific taxa within *T. cordifolia* by Lakela, who recognized two varieties (vars. *typica* and *austrina*) on the basis of relative leaf dimensions and marginal dentation, have been largely unavailing since variation in these characters is continuous (cf. Fernald, 1943). Variants in floral features include plants with extremely small flowers and short stamens (2–3 mm. long), as f. *parviflora* Fernald, plants with the capsule valves subequal, as f. *subaequalis* Lakela, and plants with the petals three-toothed at the apex, as f. *tridentata* Lakela. Further studies of variation patterns, ecology, and genetic compatibility to assess the obviously close relationship between *T. cordifolia* and *T. Wherryi* are needed to substantiate the continued recognition of two species in the Southeast.

The three or four species traditionally recognized from northwestern North America are also closely allied to one another, and Kern (1966) has treated these taxa as comprising two subspecies and two varieties of one polymorphic species, *Tiarella trifoliata* L. (incl. subsp. *trifoliata* var. *trifoliata*, *T. laciniata* Hook. as var. *laciniata* (Hook.) Wheelock, and *T. unifoliata* Hook. (incl. *T. californica* Kell.) as subsp. *unifoliata* (Hook.) Kern). Together, these taxa which have overlapping ranges are distributed from southern coastal Alaska southward along the Pacific Coast to Santa Cruz County, California, and eastward in Oregon, Washington, and British Columbia to southwestern Alberta, northern Idaho, and western Montana. The taxa differ from each other in leaf form and marginal dissection (the floral features are stable throughout) and previously were suspected of hybridizing when sympatric. Kern documented genetic compatibility between them and found no discontinuity in leaf variation. Taylor (1971a) confirmed the biological unity of the taxa chemically, but pointed out that the taxa are differentiated along an altitudinal gradient and often remain distinct in sympatric populations. He suggests that "breeding behavior and/or ecotypic distinctions are instrumental in preventing complete convergence."

The three investigated species, *Tiarella cordifolia*, *T. polyphylla*, and *T. trifoliata* sensu lato, are diploids with chromosome numbers of $2n = 14$. Matsuura & Sutô (1935), however, reported a gametic number of 9 for

plants of *T. polyphylla* and noted a tendency towards secondary chromosomal associations in pollen mother-cells.

Development of the ovule and female gametophyte in *Tiarella cordifolia* (*T. Wherryi*?) has been studied by Herr (1954), who found that the megaspores exhibit the T-shaped arrangement and the chalazal spore functions to give rise to an eight-nucleate embryo sac from which the mature Polygonum type sac develops. As in most species of *Saxifraga*, the polar nuclei fuse immediately, but in addition, the three chalazal antipodals disintegrate prior to fertilization.

Pollination ecology has not been studied in *Tiarella*, although one report lists the genus as proterogynous. Blooming from April through June, depending upon locality, the flowers of *T. cordifolia* and *T. Wherryi* appear to have no obvious adaptations for self-pollination, yet nectaries that might attract pollinating insects are not evident. Kern found the western taxa to be self-compatible but lacking mechanisms to insure self-pollination. In all species of *Tiarella* the carpels are puberulent at least at the base with glandular hairs, but it is not known whether insect-attracting substances are contained in the hairs.

The adaptive value of the two unequal wings (carpels) of capsules of *Tiarella* appears to be associated with seed dispersal. Savile (1961) has described the propulsion of seeds from capsules when drops of water land on the longer of the two wings, thereby depressing that carpel and opening the valvate capsule. If this mechanism is to be effective, it would appear that the seeds must be released before the capsules become dry and membranaceous and the valves become stiff.

Morphologically, *Tiarella* is unlike most genera of the Saxifragaceae in its stipulate leaves. This character, however, as well as floral and other vegetative similarities and base chromosome numbers, aligns the genus with *Mitella*, *Heuchera*, and several monotypic genera with two-carpellate, one-loculate ovaries with parietal placentation. Intergeneric hybrids involving *Tiarella cordifolia* and species of *Heuchera* and *Mitella* tend to support the postulated relationships and are discussed under these two genera.

Tiarella has been claimed to be both diuretic and useful in the suppression of urine and in treating gravel in the urinary tract.

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5. **Heuchera** Linnaeus, Sp. Pl. 1: 226. 1753; Gen. Pl. ed. 5. 106. 1754.

Pubescent, perennial herbs, usually from stout rhizomes or woody caudices [sometimes reproducing vegetatively by stolons]. Leaves mostly basal (occasionally cauline), long petiolate and stipulate, the stipules adnate to the petioles at the base; blades palmately veined, roundish-cordate or orbicular in outline, the margins lobed, notched, or toothed, usually with mucronate-tipped divisions. Flowers perfect, irregular or regular, in lax [or compact] pedunculate panicles of cymules, each cymule subtended by a small, persistent bract. Sepals 5, equal (and the flowers regular) or unequal (and the flowers obliquely irregular), connate below, forming a 5-lobed, often gibbous, turbinate, campanulate, urceolate [or sometimes flat to saucer-shaped] floral cup. Petals 5 [or rarely absent], inserted on the inner surface of the floral cup between the calyx lobes, greenish-white, pinkish [or purplish], linear, oblanceolate, or spatulate in outline, sometimes with coarsely fimbriate apices. Androecium of 5 included or exserted

stamens inserted on the inner surface of the floral cup, the filaments long and slender or short and cylindrical, tapering to the orbicular anthers. Gynoecium 2-carpellate, the carpels connate below with 2 slender filamentous [or short and cylindrical] styles free above and either exserted or included, terminated by capitate stigmas; ovary adnate to the floral cup (the free portion of the floral cup above the adnate region shorter than, equal to, or longer than the adnate region), partially to almost completely inferior, 1-loculate with numerous bitegmic, crassinucellar ovules on 2 parietal placentae. Fruit a 2-beaked capsule, usually exserted from the persistent floral cup, dehiscing between the indurated styles; seeds numerous, small, brownish black, ovoid-ellipsoidal with smooth, echinate, or verrucose surfaces; embryo small, straight, embedded in endosperm of the *ab initio* Cellular type. Base chromosome number 7. (Including *Oreanthus* Raf. ex Ser., *Oreotrys* Raf., and *Yamala* Raf.) TYPE SPECIES: *H. americana* L. (Name commemorating Johann Heinrich von Heucher, 1677–1774, professor of medicine in the University of Wittenberg and author of *Index Plantarum Horti Medici Academiae Wittembergensis*.) — ALUMROOT, ROCK-GERANIUM.

A strictly North American genus of perhaps as many as 55 species in five sections; seven species in the southeastern United States, two or three elsewhere in eastern North America, *Heuchera Richardsonii* R. Br. extending across the northern Great Plains, and about 35 in western North America from southern coastal Alaska to southern Mexico. Primarily distributed in unglaciated areas, *Heuchera* has its greatest diversity in the semiarid regions of western North America where three of the five sections (sects. HEUCHERELLA (Torrey & Gray) Rosend. *et al.*, HOLOCHLOA (Nutt.) Rosend. *et al.*, and RHODOHEUCHERA Rosend. *et al.*) are endemic. A second area of diversity occurs in the Southern Appalachians where species of sects. HEUCHERA (subgen. *Euheuchera* Torrey & Gray, sect. *Euheuchera* (Torrey & Gray) Rosend. *et al.*) and HERUCHEA (Torrey & Gray) Rosend. *et al.* are concentrated. Several east-west species pairs in sect. HEUCHERA, however, establish links between the two regions.

In the Southeast, Rydberg (1905) recognized 15 species of *Heuchera*, while Rosendahl, Butters, & Lakela (1936) reduced the number to seven but treated eight infraspecific taxa under five of the recognized species. Five of the species with nearly regular flowers and with the free, upper portions of the floral cups conspicuously shorter than or about equal to the inferior portion of the ovary belong to sect. HEUCHERA. *Heuchera americana* L. (*H. Cortusa* Michx., *H. glauca* Raf., *H. Curtisii* Torrey & Gray ex Gray, *H. lancipetala* Rydb., *H. calycosa* Small, *H. hispida* var. *hirsuticaulis* Wheelock, *H. hirsuticaulis* Rydb.), $2n = 14$, a late spring-blooming species that grows on clayey banks and rocky forested slopes, ranges from eastern Connecticut to southern Illinois, Missouri, and eastern Oklahoma, and southward into South Carolina, northern Alabama, Mississippi, and Arkansas. A highly polymorphic species, it was divided by Rosendahl *et al.* into six varieties, of which five have been documented within our area. Al-

though included in sect. HEUCHERA subsect. HEUCHERA (flowers regular with the floral cup conspicuously shorter to about equal to the inferior portion of the ovary), *H. americana* intergrades over a wide area in Michigan, Indiana, Illinois, Missouri, and Arkansas with *H. Richardsonii* (included in sect. HERUCHEA subsect. PUBESCENTES), and introgressant forms have been recognized as vars. *interior* Rosend. *et al.* and *hirsuticaulis* (Wheel.) Rosend. *et al.* The second species of subsect. HEUCHERA, *H. hispida* Pursh, is endemic to the mountains of West Virginia and might be expected to occur in the northern mountains in our region. Restricted to limestone and sandstone substrata, *H. hispida* is also a spring-blooming species, and it was long confused with *H. Richardsonii* (cf. Wherry, 1933, 1934).

Two of the three species included in subsect. VILLOSAE Rydb. ex Engler (flowers with the upper free portion of the floral cup much shorter than the inferior portion of the ovary and villous with long, white hairs, the leaves with acute lobes and seeds with long, sharp spines) occur in our area. Another highly polymorphic species with pinkish flowers and a turbinate-campanulate floral cup, *Heuchera villosa* Michx. (*H. macrorhiza* Small, *H. crinita* Rydb.) is comprised of three varieties that intergrade with one another both morphologically and geographically. Occurring in acidic soils, *H. villosa* is distributed in the mountains of Virginia, the Carolinas, Tennessee, Georgia and Alabama, westward through the Ohio River Valley to the Mississippi, and into eastern Missouri. *Heuchera arkansana* Rydb., a species of shaded seepage slopes (usually on sandstone substrata) differs from *H. villosa* in its distinctly campanulate floral cup, leaves with appressed fine, white hairs, and its generally shorter flowering stems. Closely allied to *H. villosa* var. *macrorhiza* (Small) Rosend. *et al.*, *H. arkansana* is known from a few scattered localities in Newton, Benton, Washington, and Franklin counties, Arkansas.

Subsect. MICRANTHAE Rydb. ex Engler includes *Heuchera puberula* Mack. & Bush and *H. parviflora* Bartling in our area. *Heuchera puberula* is a fall-blooming species that occurs on moist, shaded limestone bluffs from northern Arkansas and Missouri eastward to western Kentucky. A glandular-puberulent plant with flowers about 2 mm. long and the free portion of the floral cup about 0.3 mm. long, *H. puberula* is very close to *H. parviflora*, a more-or-less villous plant with smaller flowers (1.5 mm. long) that have an obsolescent floral cup. The typical variety of *H. parviflora* has white-villous petioles and is restricted to the mountains of North Carolina, while var. *Rugelii* (Shuttlw.) Rosend. *et al.* ranges from West Virginia southward through the mountains of North Carolina, Kentucky, and Tennessee, and westward into Indiana and Illinois. It is also known from Cherokee County, Georgia, and Etowah County, Alabama. As a subsection, the MICRANTHAE is similar to the VILLOSAE, but the lobes and teeth of the leaves are rounded, and the spines of the seeds are short or obsolete. Additional species included in this subsection are western and link the two areas.

Section HERUCHEA (Torrey & Gray) Rosend. *et al.* (plants with the

flowers moderately to very irregular and the free, upper portion of the wide, open-campanulate floral cup equal to or longer than the inferior portion of the ovary) is represented by two species, both in subsect. PUBESCENTES Rosend. *et al.*, in our area. *Heuchera pubescens* Pursh, a species with the styles becoming long exserted in fruit from the moderately gibbous floral cup is recorded from one collection in the mountains of North Carolina, while *H. longiflora* Rydb., a taxon with included or barely exserted styles and a strongly gibbous floral cup, is essentially restricted to our region. Outside of our area, *H. pubescens* occurs in Maryland, West Virginia, and Kentucky, while *H. longiflora* ranges from West Virginia and Kentucky, southward through the mountains of North Carolina and Tennessee and into northern Alabama. Both are plants of rocky ledges in deeply wooded regions and apparently prefer limestone substrata.

Although *Heuchera* is easily distinguished from other genera of the Saxifragoideae by its distinctive flowers arranged in paniculate or thyrsiform, spikelike inflorescences, few genera offer greater problems of delimitation and classification below the generic level. The early subgeneric classification of Torrey & Gray (1840), who recognized four subgenera, has been followed by most workers, but Rosendahl, Butters, & Lakela (1936) interpreted the categories as sections and added the fifth. Rydberg (1905) placed the species in ten groups of undesignated rank that have subsequently been treated as subsections.[4]

At the specific and infraspecific levels, taxonomic problems are multiplied not only because of variable diagnostic characters (e.g., pubescence, leaf shape, and floral structures that are subject to marked changes during anthesis) but also because of the extreme ease of gene flow between species and the production of intermediate and intergrading, often fertile hybrids. The stability of taxa within a given region appears to be a function of the strength of seasonal and ecological isolation. In the cordillera of the Pacific Northwest, the reticulate relationships between species are complicated further because of the topography and glacial history of the region (Calder & Savile, 1959).

With the exception of one report of $2n = 28$ for a Canadian population of *Heuchera Richardsonii* (Löve & Ritchie, 1966), all chromosome numbers recorded for the genus have been diploid, $2n = 14$. Satellites have been observed in mitotic divisions in some taxa, but a more frequent phenomenon is the occurrence of from one to four chromosomal fragments (or B chromosomes) in meiotic divisions. Jensen (1939) described irregularities in meiosis in *H. americana* that result in the noninclusion of one chromosome in one of the two daughter nuclei in the first division, yet pollen appeared to be 100 per cent normal.

The period of anthesis varies between species of *Heuchera*, with some blooming during the late spring and early summer, while others bloom later

[4] Rosendahl, *et al.* (1936, p. 1 in footnote) credit Engler (1928) with the valid publication of Rydberg's groups as subsections. Engler arranged the groups under the classical subgenera (sections) and thereby indirectly indicated their rank, but he did not specifically state what rank the groups carry.

in the summer and into the fall months. Insect pollination appears to be the general rule, and Graenicher (1907) noted a close relationship between the flowers of *H. Richardsonii* (as *H. hispida*) and a particular bee (*Calletes aestivalis* Patton). Nectar is secreted on the surface of the ovary and on the walls of the floral cup, the stigmas are receptive before the pollen is shed, and it appears that most species are adapted for cross pollination, although self-pollination may be expected in flowers with included anthers and styles.

Hydathodes have been reported in the leaves of some species of *Heuchera*, and the leaf petioles are distinctive in their three separate collateral bundles. A broad, continuous ring of fibers has been observed in the axis of investigated species, and the pith is likely to be very lacunar.

Heuchera is generally close to *Saxifraga* anatomically, but it shows chemical similarities to *Mitella* and *Tiarella*, genera with which it shares a two-carpellate, unilocular ovary with parietal placentae, stipulate leaves, and a base chromosome number of seven. The sterile intergeneric hybrid between *Heuchera* and *Tiarella cordifolia*, × *Heucherella tiarelloides* (Lemoine) Wehrhahn, also substantiates the alliance of *Heuchera* with *Tiarella*.

Although species of *Heuchera* are reputed astringents and were used as styptics in the treatment of ulcers by the Indians, current use of the plants is as garden ornamentals. Numerous garden hybrids have been developed, particularly in Europe, and most of the hybrids have as one parent *H. sanguinea* Engelmann, the pink-flowered coral-bells of old-fashioned perennial borders.

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Under family references see Baillon; Dahlgren, 1930; Dandy; Engler, 1891, 1928; Graenicher; Hamel, 1953; Jay, 1971; Knuth; Lubbock; Martin; Morf; Morvillez; Rickett, *pls. 94, 95*; Robertson; Rosendahl, 1905; Savile, 1954, 1961; Schoennagel; Skovsted; Small & Rydberg; Thouvenin; Torrey & Gray; and Wood.

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6. **Boykinia** Nuttall, Jour. Acad. Nat. Sci. Phila. 7: 113. 1834, nom. cons.

Leafy-stemmed, glandular-pubescent perennial herbs up to 8 dm. high from slender, horizontal rhizomes [or thick, scaly rootstocks]. Basal leaves orbicular or reniform in outline, long petiolate and deeply 3–5(6)-cleft, the margins incised with acute teeth, each tooth terminating in a hydathode-like structure [or lobed and the margins crenate with broad, mucronate lobes], the venation palmate; petioles dilated at base, [exstipulate or] with [foliaceous or] bristlelike stipules; cauline leaves alternate, like the basal leaves but becoming short-petiolate or sessile and reduced upwards.

Flowers perfect, in terminal and subterminal cymose panicles, initially lax and compacted, becoming expanded, secund and stiffened in fruit. Calyx of 5 sepals, densely covered with capitate glandular hairs, the sepals connate below, forming a campanulate or turbinate floral cup, the 5 lobes erect, their apices acute. Corolla regular, of 5 white [or greenish yellow] petals inserted on the rim of the floral cup, sessile or clawed, and early deciduous (in ours, one vascular trace entering the base of the petal) [or persistent]. Stamens 5, inserted opposite the calyx lobes on the rim of the floral cup and not exceeding them in length, the anthers 2-locular, white, with an apiculate appendage above, dehiscing longitudinally and long persistent, but usually deciduous before maturation of the fruit. Gynoecium of 2 follicle-like carpels, connate below and adnate to the lower 1/3–1/2 of the floral cup; styles free and divergent [or incompletely connate and erect]; stigmas inconspicuous, capitate; ovary 2-loculate with numerous bitegmic, crassinucellar, anatropous ovules on axile placentae, the placentae restricted to the connate region of the carpels. Fruit a 2-beaked, septicidal capsule within the persistent urceolate floral cup; each carpel dehiscing in the stylar region, the beaks widely spreading [or ± erect]. Seeds numerous, small, black, and shining, the surface finely granulate. Endosperm present, of the *ab initio* Cellular type; embryo small, straight; embryogeny corresponding to the Solanad type. Embryo sac of the Polygonum type. Base chromosome numbers 6 and 7. (Not *Boykinia* Raf., nom. rejic.; incl. *Therophon* Raf.; excl. *Telesonix* Rydb. and *Peltoboykinia* Hara.) TYPE SPECIES: *B. aconitifolia* Nutt. (Name commemorating Dr. Samuel Boyken, 1786–1848, planter, physician, and naturalist of Milledgeville, Georgia.) — BROOK-SAXIFRAGE.

As treated by Engler (1928), a small genus of nine or ten species; one in our region, four or possibly five in the Rocky Mountains, the Pacific Northwest, and California; one in Asia, Alaska, and the Yukon; and three indigenous to Japan. As defined by Rosendahl (1906) and Engler (1928), *Boykinia* consists of three sections, but both sectional and generic boundaries are problematic, undoubtedly because some species referred to *Boykinia* are probably best considered as species of related genera in the Saxifragoideae.

Boykinia aconitifolia Nutt. (*Therophon aconitifolium* (Nutt.) Millsp.), $2n = 12$, of our area has been placed with Pacific Northwestern and Californian species in sect. BOYKINIA, characterized by plants with divided or crenate leaves, five stamens, and gynoecia with the carpels not connate in the stylar region. Ranging in the mountains from northern Alabama and Georgia to Virginia and West Virginia, *B. aconitifolia* is a plant of moist, rocky stream banks and seepage slopes in wooded areas. Anthesis occurs in June and July, but in the vegetative phase plants of *B. aconitifolia* might easily be mistaken for plants of *Geranium maculatum* L. (Geraniaceae), which can occupy similar habitats. Plants from northern Alabama with a distinctly turbinate floral cup and rounded leaf lobes have been described

as *Therophon turbinatum* Rydb. but are probably only local variants of *B. aconitifolia*.

The affinities of *Boykinia aconitifolia* appear to be with *B. elata* (Nutt.) Greene, $2n = 14$, an extremely variable species that inhabits moist forests from middle elevations in the mountains to sea level along the coast from British Columbia south to northern California. Other western species in sect. BOYKINIA include *B. rotundifolia* Parry, endemic to the San Gabriel and San Bernardino Mountains of southern California, and *B. major* Gray, a plant that ranges from western Washington to California and northeast into Montana. *Boykinia lycoctonifolia* Engler, the sole representative of sect. BOYKINIA in Japan, has alternatively been placed in a monotypic genus, *Neoboykinia* Hara, because of its persistent greenish petals and an ovary that is almost completely adnate to the floral cup.

The two or possibly three species historically included in sect. RENIFOLIUM Rosend. are characterized by erect, partially united styles and reniform leaves. A tertiary relict endemic to unglaciated regions of Alaska, the Yukon, and the adjacent Siberian mainland, *Boykinia Richardsonii* (Hooker) Gray, $2n = 36, 84$, has five stamens and white petals and appears to be closely related to *B. rotundifolia*, a reniform-leaved species included in sect. BOYKINIA. Other species of sect. RENIFOLIUM are *B. Jamesii* (Torrey) Engler, $2n = 28$, and *B. heucheriforme* (Rydb.) A. Nelson, $2n = 14$, which are closely allied (and perhaps conspecific). Both indigenous to the Rocky Mountains from British Columbia and Alberta south to Colorado, these alpine species are characterized by purple petals and ten stamens. Treated as members of the segregate genus *Telesonix* by Rydberg, plants of these taxa are probably best considered species of either *Saxifraga* or *Telesonix*, a procedure followed in most recent manuals.

Two additional species from Japan, *Boykinia tellimoides* (Maxim.) Engl., $2n = 22$, and *B. Watanabei* Yatabe, were included in sect. PELTOBOYKINIA by Engler. Hara, however, has considered these species with peltate leaves, endosperm formation of the Helobial type, and yellowish petals covered with glandular trichomes as comprising a separate genus, *Peltoboykinia*.

Other than the reported chromosome numbers and some embryological data, biological information concerning the genus is lacking. The short anther filaments might suggest that unlike most other genera of the Saxifrageae the stamens in *Boykinia* do not exhibit the movements associated with proterandry during anthesis. Seed dispersal mechanisms have not been studied, although a mechanism in which the seeds are bounced out of the capsules by wind or passing animals is probably present. Studies of pollination ecology, dispersal mechanisms, genetic compatibility, and breeding mechanisms, as well as the use of other experimental approaches, are needed to determine the limits and homogeneity of the genus.

Species of *Boykinia* are reported to be good wildflower garden plants, but other uses of the plants have not been found in the literature.

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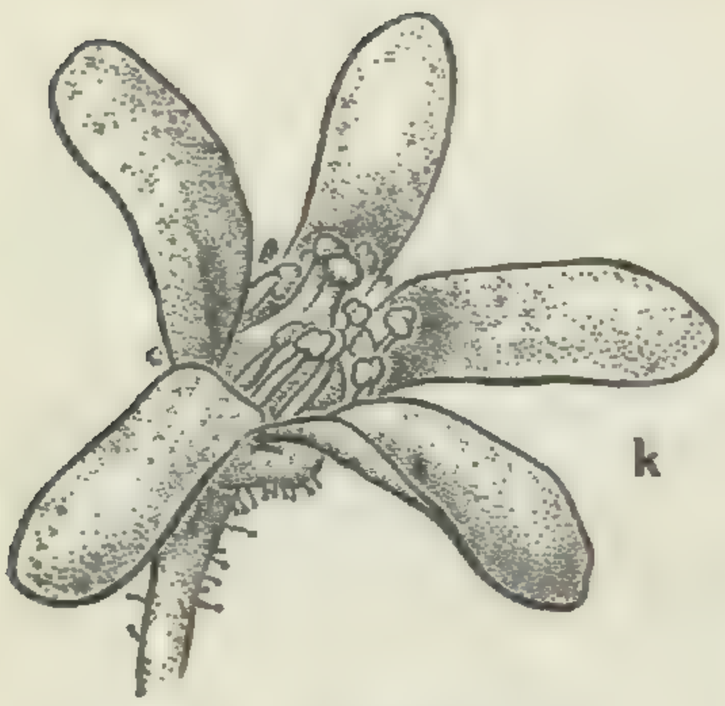
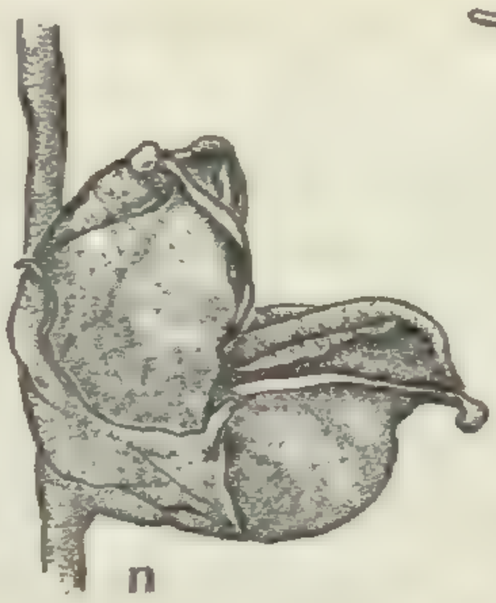
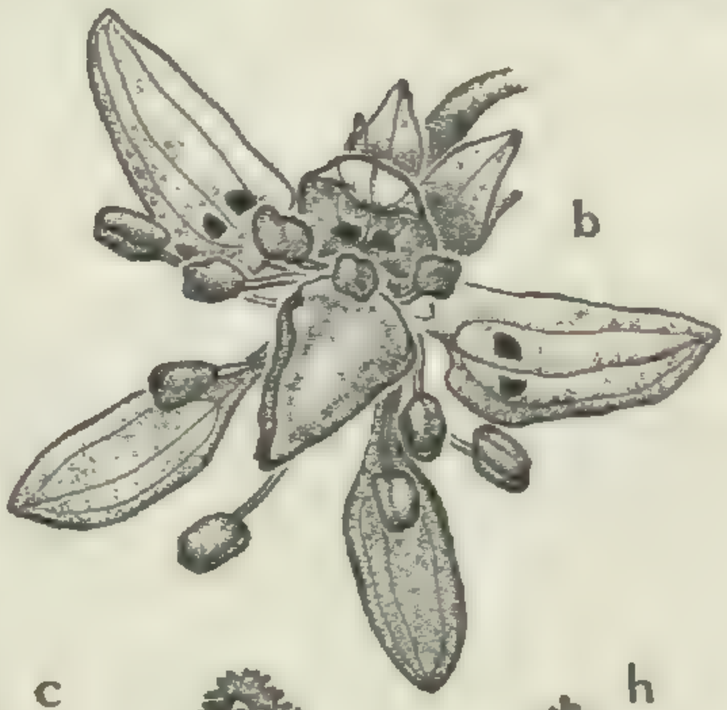
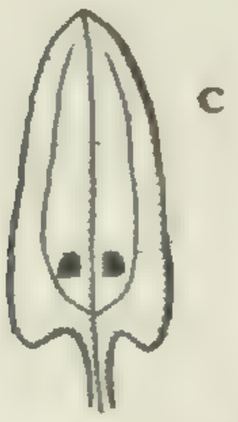
7. **Saxifraga** Linnaeus, Sp. Pl. 1: 398. 1753; Gen. Pl. ed. 5. 189. 1754.

Perennial [rarely annual or biennial] scapose [or leafy-stemmed], often evergreen herbs, commonly caespitose [or mat-forming], and generally glandular-pubescent and semisucculent [becoming woody or thickened at the base in evergreen species]. Roots fibrous, often from a rhizome [many species reproducing vegetatively by stolons and bulbils in leaf axils or inflorescences]. Leaves basal [or alternate, rarely opposite and imbricate], often red-tinged; blades with pinnate or palmate venation, ovate, spatulate, oblanceolate to lanceolate [or scalelike or peltate]; margins entire or variously dissected, usually serrate or dentate, crenate, lobed [pinnatifid, or deeply cleft]; blade tapering gradually into the petiole or constricted from an obtuse, truncate, or cordate base; foliar glands (if present) superficial or on hairs; hydathodes often along the blade margin or at the apex [in some species secreting a solution of calcium bicarbonate]. Flowers perfect, complete [or apetalous and then 4-merous], borne in racemose cymes, bracteolate panicles [or rarely solitary]; inflorescences commonly tightly compacted, at least initially, often becoming diffuse during anthesis. Sepals 5, often reflexed and united below to form a saucer-shaped [to campanulate] floral cup. Corolla white [pinkish, purple, or yellow], regular or irregular, comprised of 5 [infrequently emarginate] clawed or sessile, sometimes yellow- [or purple-] spotted petals. Androecium of 10 stamens, obdiplostemonous; anthers dehiscing longitudinally, usually deciduous; filaments slender or often clavate, persistent; pollen 3-colpate, prolate or subprolate to spheroidal. Gynoecium 2-, or 3(–6)-carpellate, the carpels free or mostly connate below the middle; styles free; stigmas usually capitate and enlarged, occasionally smaller in diameter than the style, and not infrequently decurrent on the adaxial surface of the styles; ovary superior to semi-inferior and adnate to a poorly to well-defined floral cup, 1-loculate below with parietal placentae or 2-









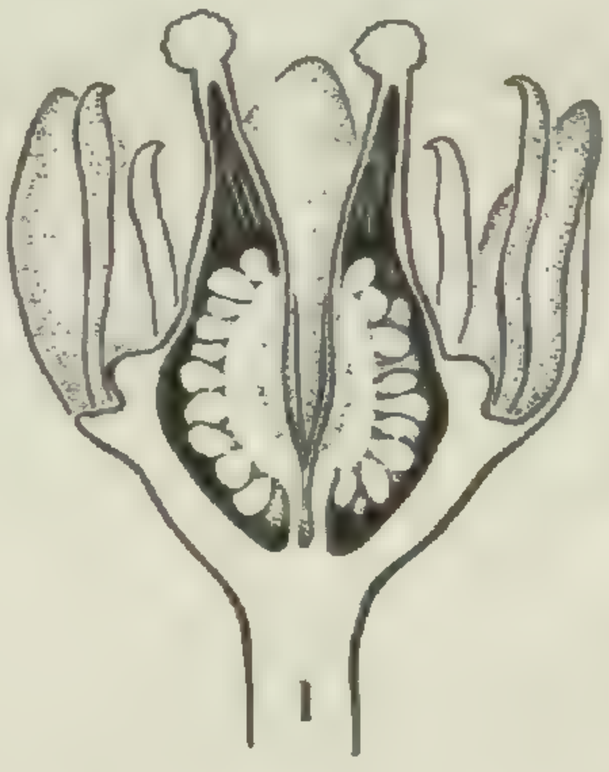


FIGURE 4. **Saxifraga.** a–i, *S. Michauxii*: a, flowering plant, × 1/2; b, flower with irregular corolla, × 6; c, d, spotted upper and unspotted lower petals, × 6; e, vertical section through immature fruit, showing placentation, × 10; f, capsule immediately before dehiscence — note reflexed sepals terminated by hydathodes, × 6; g, h, two views of seed, × 25; i, longitudinal section of seed with embryo in thin layer of endosperm, × 25. j–n, *S. virginiensis*: j, flowering plant, × 1/2; k, flower with regular corolla, × 6; l, vertical section of flower — note glandular disc at sides of ovary, × 10; m, cross section of ovary just above glandular disc (not sectioned), × 12; n, mature, dehisced capsule, × 6.

loculate with axile placentae and marginal placentae above; glandular nectar-secreting tissue sometimes present on ovary at base of styles, otherwise between ovary and the insertion of petals; ovules usually numerous, bitegmic and crassinucellar. Fruit [varying from plainly capsular and dehiscent across the top by ventral sutures of the stylar beaks (placentation axile) to] follicular and dehiscent all or part of its length; stylar beaks

erect or widely spreading at maturity. Seeds numerous, small, spinulose ribbed or glandular roughened, otherwise smooth [or the testa occasionally loose and inflated or winged]; endosperm of the Helobial type, usually copious. Base chromosome numbers 8, 9, 10, 11, 12, 13, 14. (Including *Aulaxis* Haw., *Dermasea* Haw., *Micranthes* Haw., *Spatularia* Haw., *Robertsonia* Haw., *Hydatica* Necker ex S. F. Gray, *Hexaphoma* Raf.) LECTOTYPE SPECIES: *S. granulata* L.; see J. K. Small, N. Am. Fl. 22: 127. 1905. (Name from Latin, *saxum*, a rock or stone, and *frangere*, to break, either in reference to the reputed medicinal value for kidney stones or the ability of many species to grow in rock niches and crevices.) — SAXIFRAGES.

A large genus of about 300 species grouped in from nine to 16 sections and widely distributed throughout the Arctic and North Temperate Zones. Towards the equator, *Saxifraga gemmipara* Franchet occurs in northwestern Thailand, while *S. hederifolia* Hochst. is indigenous to Ethiopia; four additional species range from Colombia to Tierra del Fuego in the South American Andes. Primarily a montane genus in the North Temperate Zone, the greatest diversity and the largest number of species occur in the mountains of Europe, where most sections are well represented. Numerous species are circumboreal, and western North America and eastern Asia are also rich in species, although only two or three sections have good representation in these regions. Seven to ten species have been attributed to the southeastern United States; upwards of 60 are known elsewhere in North America. Numerous species have xerophytic adaptations, and the genus exhibits considerable ecological amplitude in arctic-alpine environments. *Saxifraga oppositifolia* L., a polymorphic circumpolar species that occurs in alpine regions in the Temperate Zone, is known as far north in the Arctic (Kap Morris Jesup, Peary Land at 83°39′ N. lat.) as any species of vascular plant.

The eight species in our region belong to sect. MICRANTHES (Haw.) D. Don (sect. *Borophila* Engler), which is separated from other sections by characters including subterranean rhizomes, somewhat inflated capsules that dehisce above the midpoint, and a distinctive reticulate pollen sexine. Engler & Irmscher (1916) further grouped our species in three of eight *greges* below the sectional level, but Johnson (1923), utilizing other criteria, revised the North American species of this section and placed the southeastern species in five of nine new or reestablished sections.

A species of rocky outcrops in the Appalachians from Maryland to northwestern Georgia, *Saxifraga Michauxii* Britton (*S. leucanthemifolia* Michx. non LePeyr, *Hexaphoma petiolaris* Raf., *Hydatica petiolaris* (Raf.) Small, *Spatularia Michauxii* (Britton) Small) is distinguishable from other species by its irregular corolla with three petals clawed and larger than the other two, and by its ribbed spinulose seeds. Placed in sect. ARABISA Tausch by Johnson, the plants have multiseriate trichomes, superior ovaries, and elliptic capsules. In addition, the placentation is unusual, the placentae being restricted to the upper, unfused portions of the carpels and appearing marginal (cf. FIG. 4,e).

Saxifraga micranthidifolia (Haw.) Steud. (*Robertsonia micranthidifolia* Haw., *S. erosa* Pursh, *Aulaxis micranthidifolia* (Haw.) Haw., *Micranthes micranthidifolia* (Haw.) Small), $2n = 22$, restricted to moist seepage slopes and the banks of cold mountain streams from northwestern Georgia to northern New Jersey, resembles *S. Michauxii* in habit, and the two species were placed in grex *Stellares* by Engler. *Saxifraga micranthidifolia* is usually a larger plant than *S. Michauxii* and also differs in its regular corolla, clavate anther filaments, prominent disc at the base of the ovary, and smooth seeds. On the basis of its uniseriate trichomes and superior ovary, Johnson placed *S. micranthidifolia* in the monotypic sect. AULAXIS (Haw.) Johnson. Other species in grex *Stellares*, allied to our southeastern species by Engler & Irmscher, are wide ranging in Pacific North America, Asia, and Europe. The central species of the grex, *S. stellaris* L., is highly polymorphic and circumboreal.

Known in our region only from two disjunct populations in Watauga County, North Carolina, our plants of *Saxifraga pensylvanica* L. (*Micranthes pensylvanica* (L.) Haw.), $2n = 56, 84, 112$, are referable to subsp. *pensylvanica* (subsp. *eupensylvanica* Burns), $2n = 56$. The only representative of grex *Integrifoliae* Engler & Irmscher in the Southeast, this polymorphic species is wide-ranging from Maine and Ontario to Minnesota southward to Missouri and Virginia. A characteristic species of bogs, low meadows and seepage slopes, it was placed by Johnson in the re-established sect. MICRANTHES (Haw.) Tausch non D. Don, distinguished by ascending sepals and distinct carpels that are enveloped by a glandular disc or nectary. Grex *Integrifoliae*, as defined by Engler & Irmscher, is wholly North American, and the several midwestern and cordilleran species allied to *S. pensylvanica* constitute a well-defined subgrouping.

The majority of our species was included in grex *Nivali-virginiensis* by Engler & Irmscher, and, with one exception, Johnson placed the same taxa in sect. DERMASEA (Haw.) Johnson. These species, as a group, are characterized by uniseriate hairs, subinferior two-loculate ovaries, shallow floral cups, and poorly developed glandular discs. *Saxifraga virginiensis* Michx. (*Dermasea pilosa* Haw., *Micranthes virginiensis* (Michx.) Small), $2n = 28$, a plant of dryish to moist woodlands, ranges from New Brunswick to Minnesota, south to Georgia, Alabama and Mississippi. Primarily a species of the Piedmont in our area, *S. virginiensis* flowers early in the spring and has an initially compacted inflorescence that usually becomes lax and diffuse during flowering, ovaries partially adnate to the floral cup, and sepals that are ascending in fruit. It appears to be closely allied to *S. texana* Buckl. (*S. Reevesii* Cory, *Micranthes texana* (Buckl.) Small), which differs in its rhomboidal inflorescence, three- (or four-) carpellate ovary, and basal leaves with the margins entire and undulating rather than crenate, lobed, or shallowly toothed as in *S. virginiensis*. Segregated from other species and placed in the monotypic sect. TRICARPUM by Johnson, *S. texana* grows in acidic soils in sandy bottomlands, rocky glades, and on sandstone outcroppings from southwestern Missouri and adjacent Kansas southward through Arkansas, Oklahoma, and northeastern Texas.

In Missouri, it is sometimes associated with the rare *Geocarpum minimum* Mack. (Caryophyllaceae).

Saxifraga Palmeri Bush (*S. virginiensis* var. *subintegra* Goodman) is also closely allied with *S. virginiensis*. Endemic to western Arkansas and eastern Oklahoma (outside the range of *S. virginiensis*), *S. Palmeri* inhabits dryish rocky woodlands that are usually underlain by standstone. It differs from *S. virginiensis* in its entire or subentire leaves and from both that species and *S. texana*, in its glabrous or glabrate pedicels and flowering scapes. Although the ranges of *S. Palmeri* and *S. texana* overlap and seasonal isolation between them is incomplete, both flowering in spring, hybrids have not been reported. Crossing experiments and cytological studies within this group might help to clarify relationships.

Saxifraga caroliniana A. Gray (*Micranthes caroliniana* (A. Gray) Small, *M. Grayana* (Britt.) Small, *Saxifraga Grayana* Britt.) and *S. Careyana* A. Gray (*Micranthes Careyana* (A. Gray) Small) are also phenetically very similar, and it has been suggested that they may be conspecific. Unlike other southeastern species of this section in their clawed petals, they differ from one another in several details. Petals of *S. caroliniana* are yellow-spotted, the anther filaments are clavate, the sepals are strongly reflexed in fruit, and mature capsules are ca. 4–5 mm. long, while in *S. Careyana* the petals lack spots, the filaments are filiform, the sepals are more or less spreading, and the capsules are 2.5–3 mm. long. Plants from Tennessee with capsules up to 4.5 mm. long have been recognized as *S. tennesseensis* Small, but are considered by Lord as local variants of *S. Careyana*. Both *S. Careyana* and *S. caroliniana* are rare, infrequently collected plants that are restricted to moist seepage slopes and rocky stream banks in the mountains of southwestern Virginia, North Carolina, and eastern Tennessee. *Saxifraga caroliniana* has also been reported from the mountains of Kentucky. Crossing experiments and cytological studies of plants of these taxa are needed.

Our Southeastern species of grex *Nivali-virginiensis* appear to be allied with numerous species in the Cordillera of western North America where several species appear to be vicariads of our species. Additional members of this grex are circumboreal, Eurasian, or restricted to the Himalayan region.

The initial broad generic concept in *Saxifraga* established by Linnaeus was delimited more narrowly by Haworth (1812, 1821), who allocated the species among 16 genera. More recently, Small (1905) re-established several of Haworth's genera, among others, placing the North American species of *Saxifraga* in 13 segregate genera. The broad Linnaean interpretation of the genus advocated by Seringe (1830), Hooker (1865), Engler (1872, 1891), and Engler & Irmscher (1916, 1919) has been widely accepted and is strengthened by the relatively uniform floral morphology throughout the genus.

Subgeneric categories of *Saxifraga* have been problematic. Huber has revised sectional nomenclature and realigned the species into 14 sections, one of which, DISCOGYNE Sternb., was treated as a separate genus (*Zahlbrucknera* Reichenb.) by Engler. Studies of pollen fine-structure have

mainly reinforced Engler's sectional alignment, even though ". . . many of his [15] sections . . . are almost impossible to define or diagnose honestly" (Ferguson & Webb, p. 309).

Chromosome numbers reported for species of *Saxifraga* range from $2n = 16$ to $2n = 120$, and an aneuploid series from $n = 8$ to $n = 14$ constitutes base numbers for the genus. Several sections have several base numbers, including sect. MICRANTHES in which $x = 8$, 10, 11, and 14. Advanced sections (sects. AIZOÖNIA, TRACHYPHYLLUM, PORPHYRION, and XANTHIZOÖN) generally have higher base numbers, but not necessarily the highest diploid numbers, since polyploidy has been frequent in most groups.

Reports of hybrids in the genus are frequent, particularly those involving species of horticultural interest, and interspecific hybridization and the formation of fertile (or only partially sterile) progeny that may become involved in the synthesis of secondary and tertiary hybrids has been documented (Webb, 1950) in the *caespitosa* group of sect. SAXIFRAGA (sect. *Dactyloides* Tausch.). Hybrids between *S. rosacea* Moench and *S. granulata* L. have resulted in the allotetraploid *S.* × *potternensis* through nonreductional divisions at meiosis in F_1 generation plants (Marsden-Jones & Turrill, 1930; Whyte, 1930).

Observations on insect visitors to flowers of *Saxifraga* indicate that the often yellow- or purple-spotted petals and the nectar secreting region at the base of the styles or between the ovary and petals attract a predominance of dipterous pollinators. Although some species are homogamous and others are proterogynous, most species are proterandrous. In proterandrous flowers, the stamens are initially horizontal, but first the antisepalous and then the antipetalous stamens bend upward over the styles, and the anthers dehisce. Soon after the pollen is shed, the anthers are usually deciduous. Development of the styles and stigmas is usually completed after the pollen is shed, and, in the "mossy" saxifrages, the stigmas become receptive six or seven days after the onset of anthesis (Webb, 1950). Both self-compatibility and self-fertility, however, have been recorded in the genus, although compatibility systems have not been studied sufficiently.

In arctic regions species of *Saxifraga* initiate flower primordia during the growing season before that in which anthesis occurs (Sørensen, 1941), and Levin (1960) has noted well-developed flower buds in mid-November in New Jersey populations of *S. virginiensis*. In advanced flower primordia pollen tetrads may be developed before the onset of dormancy, while in other less advanced buds pollen mother cells that over-winter in some arrested stage of meiosis may be present. Meiotic abnormalities and reduced pollen fertility in several species suggest a history of hybridization, particularly in polyploid taxa, but may result from environmental factors that disrupt microsporogenesis.

Seed dispersal from dehisced capsules in *Saxifraga* is effected by short-period vibrations, which cause the seeds to bounce out of the capsules and to be carried short distances by the wind (Savile, 1961). The small seeds of *S. virginiensis* germinate in the spring on litter-free substrata, and it

has been suggested by Levin that this is a species of early stages of succession.

Aspects of megasporogenesis, embryo sac development, and embryogeny are relatively uniform in investigated species, although both unitegmic and bitegmic ovules and linear and T-shaped megaspore tetrads have been reported. Twin embryo sacs have also been recorded, and two radicles from a single seed have been noted in other species. Endosperm formation usually coincides with the Helobial pattern, although some variation is evident in the formation of so-called "basal" endosperm. At maturity, the small, straight embryo usually lies surrounded by from three to five cell layers of endosperm.

Vegetative reproduction by bulbils, vivipary, stolons, and rhizomes has been used to some extent as a criterion in delimiting sections. In arctic and boreal species vegetative reproduction sometimes completely replaces sexual reproduction in some populations, but agamospermous seed production has not been documented in the genus.

The petioles of most species of *Saxifraga* are anatomically distinctive. One or more (usually three) concentric or hemiconcentric vascular bundles, each with an endodermis, are present. Medullary bundles have been recorded in stems of *S. pensylvanica* and species of sect. Aizoönia. As in species of *Parnassia* and *Lepuropetalon*, species of sect. Cymbalaria develop tanniniferous cells in the epidermis, but the ontogeny of these deviates from the developmental pattern in the other genera. The stomata, generally of the ranunculaceous type, have been considered of diagnostic value, since species groups can be defined by stomatal distribution patterns. Trichome types that vary from uniseriate or biseriate to multiseriate are also of taxonomic significance. Hydathodes along leaf margins and at sepal and leaf apices are also relatively common in the genus, and three types have been described. Termed chalk glands when their secretions contain calcium bicarbonate, the hydathodes exude a concentration of calcium that is apparently determined by soil chemistry (Kurt, 1929). Schmidt (1930) has observed that in certain European species guttation from hydathodes occurs only before the onset of anthesis and that the amount of fluid secreted is determined by a combination of light, temperature, and humidity factors.

Pollen structure in the genus is heterogeneous, but the recent survey of pollen fine-structure by Ferguson & Webb (1970) revealed four distinct types of sexine pattern that aid in the division of the genus into sections and that should prove helpful in solving taxonomic and paleoecological problems. Section Micranthes, to which our species belong, is distinguishable from other sections by a reticulate pollen sexine, and pollen from *Saxifraga micranthidifolia* is the smallest (polar axis 15–16.5 μm) noted in the survey. Pollen size, however, does not appear to be correlated with chromosome number (Sokolovskaia, 1958).

Determination of the generic relationships of *Saxifraga* is dependent, in part, on the definition of generic bounds. Aside from the several segregate genera that rarely remain distinctive when considered in the over-all view

of the genus, *Saxifraga* appears to be most closely allied to the Asian genus *Bergenia* Moench, to *Saxifragella* Engler (two species in Tierra del Fuego), to *Leptarrhena* R. Br. (monotypic, ranging from Alaska to Washington), and to *Heuchera*. Because of the great species diversity and sectional representation, the mountains of Europe have been considered a primary center of evolution for the genus. The least specialized species, however, are probably in Japan and neighboring regions, and, judging from the great development of subfam. Saxifragoideae in western North America, Savile (1961) has postulated that *Saxifraga* had its origin in a primitive East Asian immigrant group that through a series of Cordilleran radiations into North America also gave rise to the several endemic North American genera.

Many species of *Saxifraga* are cultivated in rock and alpine gardens, and numerous hybrids have been produced both spontaneously and through breeding programs. The easily hybridized species of *Bergenia* are also occasionally cultivated in rock gardens and may be confused as species of *Saxifraga*. *Saxifraga stolonifera* Meerb. (*S. sarmentosa* Schreder in Ellis), a native of China and Japan, is the old-fashioned pot plant known as strawberry begonia, strawberry geranium, or mother-of-thousands.

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8. **Chrysosplenium** Linnaeus, Sp. Pl. 1: 398. 1753; Gen. Pl. ed. 5. 189. 1754.

Small, fibrous-rooted, sometimes semi-aquatic perennial herbs, decumbent and creeping [or caespitose]; stems often becoming stoloniferous [or rhizomatous, sometimes producing bulbils]. Leaves opposite [or alternate], subsessile to distinctly petiolate; basal and cauline leaves isophyllous [or heterophyllous], blades simple, the margins crenate [or toothed], rarely entire. Flowers perfect, regular, inconspicuous, greenish-yellow [white or purplish], [terminal and solitary or] arranged in loose [or compact], often leafy dichasial cymes. Calyx of 4 spreading [or ascending] sepals, connate below and forming a campanulate [or saucer-shaped] floral cup; one pair of sepals larger than the other pair and overlapping it in the bud. Petals absent. Stamens (7) 8 [4 or 10], corresponding to the number of disc lobes (if the disc is developed); filaments inserted on the mar-

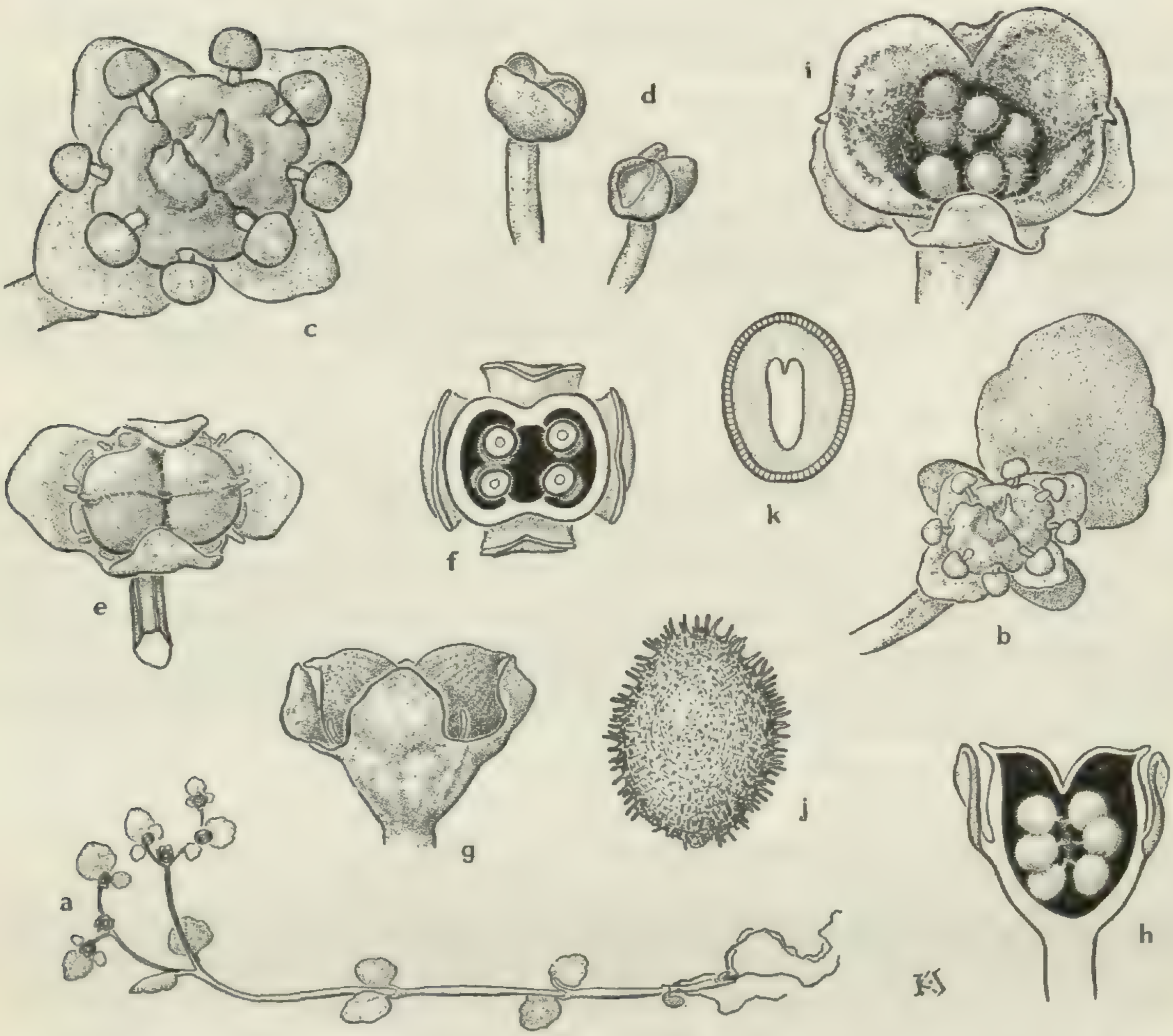

FIGURE 5. **Chrysosplenium.** a–k, *C. americanum*: a, habit, × 1/2; b, flower with subtending leaf, × 6; c, flower in early stage of anthesis showing large, lobed disc, × 12; d, detail of dehisced anthers, × 25; e, capsule seen from above before dehiscence — note shriveled disc, × 6; f, semidiagrammatic cross section of capsule showing parietal placentae, × 6; g, side view of two-beaked capsule, × 6; h, semidiagrammatic vertical section of undehisced capsule, × 6; i, dehisced "splash-cup" capsule from above, × 6; j, seed, × 25; k, semidiagrammatic longitudinal section of seed with embryo embedded in endosperm, × 25.

gin of the disc [or floral cup]; anthers red [or yellow], 2-loculate, dehiscing laterally; pollen 3-colporoidate, subprolate. Gynoecium of 2 carpels; styles free; ovary [superior to] inferior, ± adnate to the floral cup [or free], surrounded by and partially embedded in the disc, uniloculate, with several anatropous ovules on 2 parietal placentae. Disc nectar-secreting, well developed [or absent], often lobed and colored purplish [or greenish-yellow], becoming shriveled and obscured in fruit by the enlarging ovary. Fruit a subinferior capsule with 2 short, divaricate beaks, dehiscing between the styles along lines above the 2 placentae, flaring, and appearing cup shaped. Seeds numerous and small, oblong [to globose] with a distinct keel on one side, reddish brown [or black]; surface [smooth, ridged, or] verrucose, usually with papillae; endosperm of the Helobial type, copious, surrounding the small, straight embryo. Base chromosome number 6 or 7. LECTOTYPE SPECIES: *C. oppositifolium* L.; see J. K. Small & P. A. Rydberg, N.

Am. Fl. 22: 83. 1905. (Name from Greek, *chrysos*, gold, and *splen*, spleen, in reference to the plant's alleged medicinal attributes.) — GOLDEN SAXIFRAGE.

A genus of about 55 species widely distributed in the Arctic and Temperate zones of the Northern Hemisphere and two species disjunct in the Southern Hemisphere, occurring in the Andes of Chile and in Patagonia and Tierra del Fuego. The greatest number of species occurs in eastern Asia where about 27 are indigenous to the Sino-Himalayan region and 10 are native in the Japanese flora. *Chrysosplenium americanum* Schweinitz ex Hooker, $2n = 24$, is the sole representative of the genus in our region, but five additional species are known from North America. Reported from scattered localities in the mountains of Georgia, North Carolina, and adjacent eastern Tennessee, *C. americanum* is a plant of moist stream beds, stream banks, and wet forests, a habitat to which all species of the genus appear to be restricted. Sometimes semiaquatic, plants of *C. americanum* often form extensive populations in the shallow waters of brooks and streams and at first glance might be mistaken for watercress, *Nasturtium officinale* (*Rorippa Nasturtium-aquaticum*, Cruciferae). Outside our area, *C. americanum* is known from stations northward along the Appalachians into New England, Nova Scotia, and the Gaspé Peninsula, westward through Quebec to Saskatchewan and southward around the Great Lakes in Minnesota, Wisconsin, Illinois, Indiana, Michigan, and Ohio.

The affinities of *Chrysosplenium americanum* do not appear to be with the only other opposite-leaved species in North America, *C. glechomifolium* Nutt. ex Torr. & Gray, indigenous to the Pacific Coast States and British Columbia, but instead with *C. oppositifolium* L., widespread in Europe, and with *C. ramosum* Maxim., known from Hokkaido and the mountains of Korea north to the mountains of the Amur region. According to Packer (1963), the alternate-leaved North American species include *C. tetrandrum* (Lund) T. Fries, a circumpolar plant also known from disjunct populations in the Colorado Rockies; *C. Rosendahlii* Packer, endemic to the Canadian Arctic Archipelago and the adjacent mainland; *C. iowense* Rydb., originally thought to be restricted to the driftless area of northeastern Iowa but later shown to be more widely distributed in the plains of southwestern Manitoba, central Saskatchewan, and Alberta, north to the vicinity of Great Slave Lake; and *C. Wrightii* Franchet & Savatier, known from Alaska and Herald Island off the arctic coast of Siberia. The taxonomy of *C. tetrandrum*, *C. Rosendahlii*, and *C. iowense* has been complicated inasmuch as the species form a complex that has close affinities with the Old World *C. alternifolium* L. Packer (1963), who has clarified this situation, says that biosystematic investigations are still necessary within the broadly defined species, *C. alternifolium*.

The subject of three monographs, *Chrysosplenium* has been divided into two subgenera and several series by Maximowicz (1881); two sections by Franchet (1890, 1891), and seventeen series by Hara (1957).

Hara concluded that the subgenera *Chrysosplenium* (subgen. *Gamosplenium* Maxim.) and *Dialysplenium* Maxim. and the sections CHRYSOSPLENIUM (sect. *Oppositifolia* Franch.) and ALTERNIFOLIA Franch. are unnatural and polyphyletic assemblages based on variable floral and foliar characters, respectively. Franchet's division of the genus into alternate-leaved and opposite-leaved species, although not formally recognized by Hara, is nonetheless employed by him and seems to be of value when dealing with the species on a world-wide basis. Furthermore, leaf arrangement has been correlated with two types of stomatal development (Moreau, 1971). Collectors should make notes from unpressed material, since the flowers are small and delicate, and diagnostic floral features are often obscured in the preparation of herbarium specimens.

Little biological information is recorded about the species of *Chrysosplenium*. Chromosome numbers are known for only eight species, yet cytologically known taxa include all the North American species except *Chrysosplenium glechomifolium*. A wide range of numbers is evident: *C. americanum*, *C. Wrightii*, *C. tetrandrum*, and *C. nepalense* D. Don have reported numbers of $2n = 24$, while other counts include $2n = 22$ for *C. Grayanum* Maxim., $2n = 42$ for *C. oppositifolium*, $2n = 48$ for *C. alternifolium*, $2n = 96$ for *C. Rosendahlii*, and $2n =$ ca. 120 for *C. iowense*. Although Hamel (1953) notes that the chromosomes are extremely small and difficult to distinguish from one another, he suggests on the basis of chromosome morphology that *C. alternifolium* is an autotetraploid.

The few recorded observations suggest that the reproductive biology of *Chrysosplenium* is varied and probably subject to environmental and seasonal modification. In Greenland, Sørensen (1941) observed development of flower primordia and pollen formation in the fall in plants of *C. tetrandrum*. Anthesis occurs in early spring, and the flowers have been variously described as homogamous, proterogynous, or proterandrous. The disc, when developed, is nectar secreting, and the flowers appear adapted to pollination by a wide range of short-tongued insect visitors. Müller (1883), in addition, reported that pollination of *C. alternifolium* is often effected by young snails (*Succinea* sp.) that traverse the open flowers leaving a film of mucus. Self-pollination is apparently prevalent, at least in arctic species, and Kobus (1883) reported that *C. oppositifolium* becomes andromonoecious when growing in dense colonies. Once flowering has been completed, the plants often exhibit great vegetative variation, probably induced by the gradual drying of the substratum in which the plants are growing. Sterile branches often become decumbent, and vegetative reproduction is effected by stolons, rhizomes, and occasionally bulbil formation.

The seed dispersal mechanism in *Chrysosplenium* is related to the parietal position of the placentae. In *C. americanum* the fully dehisced capsule has the shape of a deep cup with a flared rim. The capsule opens along lines between the styles down to a point above the two placentae, thereby exposing the seeds on the wall below, and forming a "splashcup" that resembles the gemma cups of *Marchantia*. In a laboratory experi-

ment, Savile (1953, 1961) found that a drop of water landing in the cup caused the ripened seeds to be thrown horizontally up to a distance of 16 inches. In nature the mature capsules are held upright, positioned, as it were, to catch falling drops of rain; and as Savile points out, "*Chrysosplenium* is well suited to this dispersal mechanism since it grows frequently in the splash from waterfalls, below moist cliffs, or in swampy woods where even a drizzling rain will fall from the trees in large drops." The seeds, which offer diagnostic characters due to their sculptured surfaces, have been germinated on moist filter paper after dormancy has been broken by chilling.

The affinities of *Chrysosplenium* are not clearly evident within the Saxifragaceae, although tannin sacs in the epidermis of many species suggest relationships with *Saxifraga* sect. CYMBALARIA, and the genus has consistently been placed in the Saxifrageae DC., subtribe Saxifraginae Engler. The presence of hydathodes in leaves of some species also tends to support this placement, but chemically *Chrysosplenium* is remote from other genera of the subtribe (Jay, 1970).

No reports of economic use of *Chrysosplenium* have been located, but the plants have been used as salad greens and might constitute an emergency survival food.

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Subfam. PARNASSIOIDEAE Dandy

9. **Lepuropetalon** Elliott, Sketch Bot. S. Carolina Georgia 1 : 370. 1817.

Diminutive, leafy, acaulescent or branched winter annuals from slender primary roots and poorly developed basal rosettes, usually forming small hemispherical tufts. Leaves alternate or subopposite, spatulate, the blade constricted into a broad petiole; margins entire, apex acute or obtuse; plants glabrous but with conspicuous golden-brown tannin sacs in the epidermis. Flowers perfect, small and inconspicuous, either appearing sessile in the basal rosette or terminal at the ends of short, leafy, and angled stems. Calyx of 5 broad, persistent, often unequal sepals with acute or obtuse apices, the sepals connate below, forming a campanulate, 5-ribbed floral cup. Corolla sometimes absent or of (4) 5 linear, bractlike, submicroscopic white petals alternating with the sepals, inserted on the rim of

FIGURE 6. **Lepuropetalon.** a–l, *L. spathulatum*: a, upright, branched plant, × 5; b, habit of small tufted plant with numerous flowers, × 2; c, leaf, showing pattern of epidermal tannin sacs, × 6; d, flower at onset of anthesis with anthers above styles, × 20; e, later stage of anthesis showing staminodia and petals behind stamens, × 20; f, detail of stamen, × 25; g, vertical section of flower showing parietal placentae and (on right) insertion of petal and staminodium, × 15; h, cross section of ovary, × 10; i, dehisced capsule with persistent calyx, × 12; j, seed, × 50; k, cross section of seed, × 75; l, embryo oriented as in seed, × 50.

the floral cup. Androecium dimorphic, of 5 staminodia opposite and inserted with the petals and 5 functional stamens opposite the sepals, the staminodia dilated distally, the filaments of the functional stamens short; anthers globose, yellow, 2-loculate at anthesis, dehiscing longitudinally; pollen 3-colporate, subprolate, finely reticulate. Gynoecium 3-carpellate, the 3 commissural stigmas free, the styles ± connate below; ovary inferior, adnate to the floral cup, 1-loculate with numerous anatropous ovules on 3 parietal placentae. Fruit a loculicidal capsule, the seeds numerous, minute, cylindrical (0.15–0.2 mm. long × 0.07–0.1 mm. broad) with a short beak

at one end, the surface reticulate, red-tinged when immature, blackish when ripe; embryo straight, endosperm scanty. TYPE SPECIES: *L. spathulatum* (Muhl.) Ell. (*Pyxidanthera spathulata* Muhl.). (Name from Greek, *lepyron*, a shell or husk, and *petalon*, a leaf or petal, apparently in reference to the inclusion of the small petals within the persistent sepals.)

One species, *Lepuropetalon spathulatum* (Muhl.) Ell., occurring in three widely separated regions: in the southeastern United States and Mexico, in central Chile, and in Uruguay. A diminutive herb up to 2 cm. high, *L. spathulatum* grows in wet sandy soils in cemeteries, pastures, along power lines, and at the edges of earth-filled depressions on rock outcrops from New Hanover County, North Carolina, southward on the Coastal Plain (rarely on the Piedmont) through South Carolina, Georgia, Alabama, Louisiana, and eastern Texas and along the Gulf Coast in Mexico. Undoubtedly overlooked by collectors due to its small size and early flowering period, *Lepuropetalon* ranks as one of the smallest terrestial flowering plants. It is probably more abundant and widespread in the Southeast than herbarium collections indicate (cf. Thomas, 1971), and it may be found associated with species such as *Hedyotis* (*Oldenlandia*) *crassifolia*, *Krigia virginica*, *Trifolium carolinianum*, *Plantago heterophylla*, *Tillaea aquatica*, and *Anagallis* (*Centunculus*) *minima*.

Essentially unknown biologically, the fact that *Lepuropetalon* is a winter annual suggests that the plants are self-compatible and that the flowers are probably self-pollinated. Observations on a series of plants preserved in alcohol support this hypothesis and show that at the onset of anthesis (FIG. 6d) the anthers dehisce while positioned directly over the stigmas. At progressively later stages of anthesis (FIGS. 6e & f) the ovary swells and the anthers are "pushed" to the sides of the ovary. The mature capsules dehisce in spring, but germination of the numerous seeds is delayed until mid-winter when dormancy is broken, probably in response to increasing day length.

Engler (1891) originally placed *Lepuropetalon* in the Saxifraginae of subfam. Saxifragoideae but later (1928) isolated the genus in a separate subfamily and tribe, the Lepuropetaloideae Engl., tribe Lepuropetaleae Engl. Nakai (1943) went a step further and established the family Lepuropetalaceae. On the basis of morphological similarities (cf. Murbeck, 1918), Dandy (1927) placed *Lepuropetalon* with *Parnassia* when he established the Parnassioideae. With *Parnassia*, *Lepuropetalon* shares its dimorphic androecium, the presence of the same type of tannin sacs in the epidermis, and its commissural stigmas, a character known elsewhere only in the Papaveraceae. A chromosome count might further substantiate this placement.

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10. **Parnassia** Linnaeus, Sp. Pl. 1: 273. 1753; Gen. Pl. ed. 5. 133. 1754.

Fibrous-rooted herbaceous perennials, usually developing stout rhizomes or rootstocks; plants glabrous, but with tannin cells evident in the epidermis, these often imparting a rusty appearance to the foliage. Basal leaves petiolate, the blades palmately veined, ovate, reniform, or orbicular, with entire margins and cuneate, truncate, or cordate bases. Flowers perfect, borne individually on scapiform stems with 1 cauline leaf [or many cauline leaves in sect. Fimbripetalum] like the basal leaves but reduced and sessile, often with a clasping base. Calyx of 5 broad, persistent sepals, connate below, forming a poorly defined floral cup. Petals 5, showy and white [yellowish or pink], the laminar surface furrowed over the conspicuous, greenish, parallel veins; margins entire [or fimbriate at the base], sessile or clawed. Androecium consisting of 5 staminodia opposite the petals (the column of each divided into 3 [or many] filiform divisions with glandular-appearing apices) and 5 functional stamens alternating with the staminodial whorl and the petals; anthers large, tetrasporangiate, ovate or oblong with a cordate base; pollen 2-celled when shed, 3-colporate, sometimes syncolpate or 4-ruporate, oblate spheroidal or prolate. Gynoecium [3- or] 4-carpellate, the stylar region short or absent, the [3 or] 4 commissural stigmas expanding and becoming distinct during anthesis; ovary superior or partially inferior and adnate to the floral cup, ovoid, 1-loculate, with numerous bitegmic, anatropous, tenuinucellar ovules on [3 or] 4 dilated parietal placentae, the placentae continuous with the exposed stigmatic surfaces above. Fruit a loculicidal capsule opening at the apex by four valves; seeds numerous, sawdust-like, with a loose, wing-like testa; embryo small, straight, with short cotyledons; endosperm of the *ab initio* Cellular type scanty or absent; embryo sac of the Polygonum type; embryogeny corresponding to the Asterad type; germination epigeous. Base chromosome number 9. Type species: *P. palustris* L. (Named after Mount Parnassus, the slopes from which Dioscorides reported and described a plant, the Grass-of-Parnassus. Cf. R. T. Gunther, *The Greek herbal of Dioscorides. frontisp.* xii + 701 pp. Oxford. 1934.) — Grass-of-Parnassus, bog-stars, white liverwort.

A genus of about 50 species widely distributed in wet and boggy soils in the Arctic and Temperate zones of the Northern Hemisphere; three late-summer blooming species in our region and eight or nine elsewhere in the United States and Canada. All of the North American species belong to sect. Parnassia (sect. *Nectarodroson* Drude), while other species in this

section are trans-Eurasian at high latitudes. Four additional sections of the genus as delimited by Drude (1875) and Engler (1928) are confined to the Old World where the genus exhibits its greatest diversity in the Himalayan region.

In the Southeast, the most easily distinguished species is *Parnassia asarifolia* Vent., a plant with orbicular or reniform leaves that resemble those of *Asarum* (Aristolochiaceae). The flowers of *P. asarifolia* have clawed petals, and the staminodia, which are shorter than the functional stamens, have the divisions terminated by glandular-appearing knobs. A relatively rare species, *P. asarifolia* grows in wet boggy soils and on seepage slopes at scattered localities in the mountains from West Virginia southward through Virginia, Kentucky, Tennessee, the Carolinas, and onto the Piedmont in Georgia, Alabama, and west into eastern Texas, where it grows in broad-leaved-evergreen bogs.

The two additional species in our area resemble one another closely (both have ovate basal leaves with cuneate or truncate bases, staminodia longer than the stamens, and sessile petals) but are largely separated geographically and by differences in floral structure. *Parnassia grandifolia* DC. grows in wet, circumneutral soils from northern Florida westward to Louisiana, Arkansas, eastern Texas, and Missouri, and northward in the mountains in the Carolinas, Tennessee, and Virginia. It has also been reported from West Virginia. Flowers of *P. grandifolia* have the staminodial divisions distinctly knobbed at the apex, the ovary is greenish, and the anthers are reddish, while in flowers of *P. caroliniana* Michaux (*P. floridana* Rydb.) the staminodial divisions are tapered to an only slightly enlarged, often involute apex, the ovary is whitish, and the anthers are yellow. A plant of acid soils, *P. caroliniana* occurs infrequently on the lower Piedmont and on the Coastal Plain in savannahs in the Carolinas, Florida, and Mississippi.

A fourth species of the eastern United States, *Parnassia glauca* Raf. (*P. americana* Muhl.) is widespread and relatively common from New Jersey and Pennsylvania, westward into Iowa and northward into eastern Canada. Considerable confusion has resulted because of its similarity to *P. caroliniana* and *P. grandifolia* (cf. Alexander, 1934; Wherry, 1936), but *P. glauca* can be distinguished from our species by its staminodia, which are shorter than the stamens. Cytological and biosystematic studies to elucidate the close relationships between these three species would be desirable.

Although chromosome numbers have not been determined for any of our species or for *Parnassia glauca*, cytological studies of seven or eight species have established the base number as nine and have disclosed the presence of triploids ($2n = 27$), tetraploids ($2n = 36$), and hexaploids ($2n = 54$), as well as diploids ($2n = 18$) within the genus. *Parnassia palustris* L. sensu lato (incl. *P. obtusiflora* Rupr.) includes plants of all polyploid levels (cf. Banach-Pogan, 1956; Erlandsson, 1942; and Löve, 1950), but the tetraploid (circumpolar) and diploid (trans-Eurasian and Alaskan) races are most widely distributed. The occasional triploids and hexaploids have apparently resulted from hybridization and chromosome doubling.

The intricacy of the flowers of *Parnassia* undoubtedly accounts for the long and continued interest in their floral biology. Early observers considered the flowers proterandrous since there appears to be a distinct staminate phase (during which an individual stamen curves upward and inward over the stigma, its anther dehisces while over the stigma, and the stamen moves back into rank, followed by the next stamen until all five have completed the cycle) followed by the visible outfolding and apparent maturation of the stigmas. According to the so-called "classical" theory based on these observations, the flowers are considered to be adapted for cross-pollination. Experimental studies with *P. palustris*, however, have shown that the dichogamy is imperfect and that the stigmas are receptive when the anthers dehisce; self-pollination and self compatibility have been demonstrated, but the plants are cross-compatible as well. The flowers are visited by numerous species of Hymenoptera, Lepidoptera, and especially Diptera, which are probably attracted by the staminodia in combination with the prominently veined petals that together act as nectar guides. Nectar is not secreted by the often glandular-appearing staminodial apices (and the flowers have therefore been termed deceptive) but is produced either at the base of the staminodial columns or in two basin-like folds of tissue on the adaxial surface of the columns.

Anatomically, the staminodia represent a whorl of the androecium, and the stamens of *Parnassia* are unique in the centripetal development of xylem in the single vascular bundle of the filament. Although it is perhaps not directly correlated with the stamen movements during anthesis, Arber (1913) has suggested that the hollow cylinder, which results from exarch xylem development, gives the filaments greater elasticity. The scapiform flowering stems of *Parnassia* have a well developed endodermis, the nodes are polystelic, and stomata, of the ranunculaceous type, occur on both surfaces of the leaves.

Although somewhat anomalous within the family, *Parnassia* was accommodated in the Saxifragaceae by Engler (1891, 1930), who first placed the genus in a tribe, the Parnassieae Engl., in the Saxifragoideae but later included it in its own subfamily, the Parnassioideae Dandy. On the basis of close generic similarities, Dandy (1927) had included both *Parnassia* and *Lepuropetalon* (*q.v.*) in the Parnassioideae. First included in the Saxifragaceae by Bentham & Hooker (1865), *Parnassia* had previously been most consistently allied with *Drosera* (Droseraceae), although S. F. Gray had established the monotypic Parnassiaceae as early as 1821. Later workers, each using different evidence, have either supported previous placements for the genus or suggested other affinities. Pace (1912), using embryological evidence, concluded the genus was closely allied with the Droseraceae. Arber (1913), who interpreted the androecium of *Parnassia* to be a greatly reduced phalange of stamens like those in *Hypericum*, pointed to affinities within the Hypericaceae. Lebègue (1953), on the other hand, concluded that the embryogeny of *Parnassia* (of the Asterad type) is unlike that of either the Saxifragaceae or Droseraceae but conforms most closely with development in *Claytonia* (Portulacaceae) and the Poly-

gonales, Chenopodiales, and Caryophyllales. Chemical evidence summarized by Jay (1971) shows great similarities between *Parnassia* and *Hypericum*. Undoubtedly because of the conflicting evidence of relationship and its morphological distinctiveness, the tendency in most recent manuals and floras has been to recognize the Parnassiaceae, although Cronquist has retained *Parnassia* within the Saxifragaceae. Takhtajan (1959, 1969), who recognizes the Parnassiaceae, considers the affinities between *Parnassia* and *Drosera* as indicating that his Nepenthales are possibly derived from within the Saxifragales.

Leaves of *Parnassia* contain a catechol-type tannin, a bitter principle, traces of a resin, and rutin. The plants have occasionlly been used medicinally as sedatives for heart palpitation and epilepsy and in cases of diarrhea and menorrhagia. Other uses of the plants have not been reported, although they make attractive late-blooming additions to boggy wild-flower gardens.

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Subfam. RIBESIOIDEAE Engler

11. **Ribes** Linnaeus, Sp. Pl. **1**: 200. 1753; Gen. Pl. ed. 5. 94. 1754.

Erect, arching, trailing, or prostrate shrubs [occasionally becoming arborescent], often with conspicuous 3-forked or simple nodal spines and smaller, internodal bristles. Stems decurrently ridged from nodes and epidermis usually shredding in long strips; lateral buds small, solitary; leaf scars sessile or slightly elevated, crescent or U-shaped, with 3 bundle scars; pith terete or stellate, commonly spongy; nodes trilacunar. Leaves deciduous [rarely persistent] alternate (particularly on new growth) and/or in clusters on short, alternate lateral shoots; petioles exstipulate but often dilated at base; blades plicate or convolute in bud, palmately lobed [or rarely unlobed], with palmate venation and serrate or serrulate [rarely entire] margins; hydathodes associated with the apiculate marginal teeth. Flowers perfect [or imperfect by abortion and the shrubs dioecious], occurring singly, in few- to many-flowered, often bracteate axillary racemes [or in umbellate infloresences]; each pedicel with a clasping, foliaceous bract at about its midpoint, and jointed or unjointed beneath the ovary. Calyx of [4 or] 5 greenish, yellow [white or red to pink or wine-colored] sepals, adnate to the ovary and connate above, forming a turbinate, campanulate [rotate], or tubular floral cup, the calyx lobes usually reflexed. Petals [4] 5, colored like calyx or of contrasting color, often changing with age, smaller [or larger] than calyx lobes and inserted on inner surface of floral cup [or occasionally lacking]. Androecium of [4] 5 included or exserted stamens, inserted on inner surface of floral cup and alternate with petals; filaments pubescent or glabrous, thin and tapering to the oblong or subglobose anthers that dehisce by longitudinal slits; pollen yellow [or white], spheroidal, 8- or 9-aperturate, 2-celled when shed. Gynoecium 2-carpellate, syncarpous; styles 2, included or exserted, often surrounded by an annular disc at the base of floral cup, [free or] connate for all or part of their length, terminating in a single, capitate or bifid stigma; ovary inferior, 1-loculate with few to many anatropous, bitegmic, crassinucellar ovules in 2 or more series on each of 2 parietal placentae. Fruit a spiny, bristly, glandular-pubescent or glabrous red [yellow], greenish, or purplish-black berry, terminated by the withered remains of the flower and

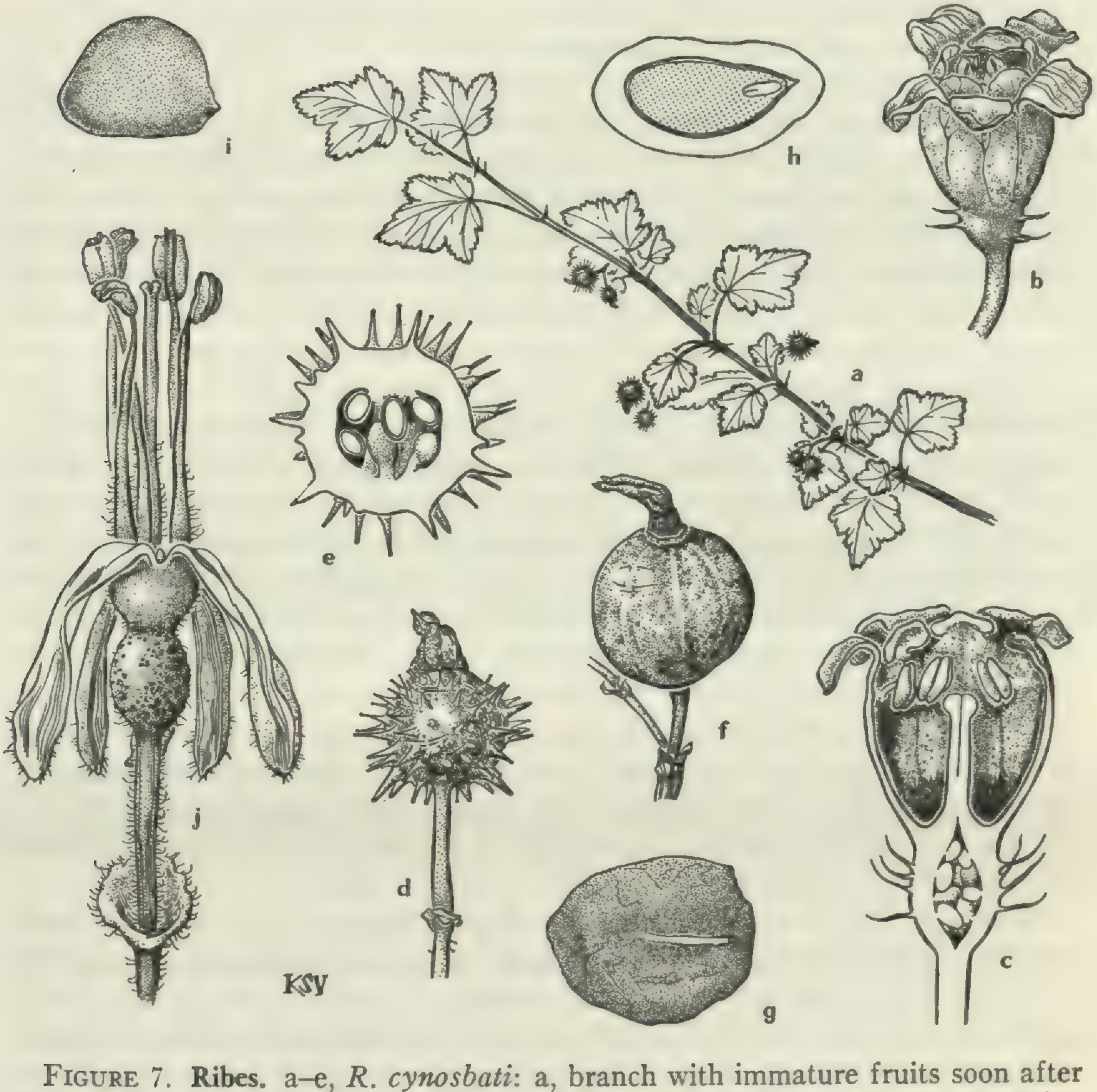

FIGURE 7. **Ribes.** a–e, *R. cynosbati*: a, branch with immature fruits soon after anthesis, × 1/4; b, flower, × 5; c, vertical section of flower showing insertion of anthers and petals and parietal placentae, × 6; d, immature fruit with persistent calyx, × 2; e, cross section of immature fruit, × 3. f–i, *R. rotundifolia*: f, mature fruit with persistent, shriveled calyx, × 2; g, seed with pulpy aril, × 10; h, longitudinal section of seed and aril (unshaded) showing embryo embedded in endosperm (stippled), × 10; i, seed with aril removed, × 10. j, *R. curvatum*: flower, showing exserted anthers and style and sessile glands on the ovary, × 5.

disarticulating when ripe if pedicel is jointed. Seeds few to many, irregularly elliptic-ovate, with a hard, brownish seed coat; each seed coated by a pulpy, gelatinous substance (aril) developed from the funiculus, the pulp filling the cavities of the fruit between individual seeds; embryo small, straight, embedded in copious endosperm of the *ab initio* Cellular or Helobial type. Base chromosome number 8. LECTOTYPE SPECIES: *R. rubrum* L.; see F. V. Coville & N. L. Britton, N. Am. Fl. 22: 193. 1908. (Including *Grossularia* Miller, *Rebis* Spach, *Coreosma* Spach, *Chrysobotrya* Spach.) (Name of uncertain origin, but probably originally derived from Arabic, *rībās*, the colloquial name for Arabian rhubarb, *Rheum Ribes* L.,

a plant from which a red syrup, similar to currant syrup, was prepared for medicinal use.) — CURRANTS, GOOSEBERRIES.

A genus of about 150 species, alternatively placed in two genera (*Ribes* sensu stricto and *Grossularia* P. Miller) and widely distributed in the North Temperate Zone of Eurasia, in the Mediterranean region of northwestern Africa, in North America from Labrador to Alaska, southward through Mexico, and in the Andes from Venezuela and Colombia to Patagonia. Assignment of currants (flower pedicels jointed) to *Ribes* and gooseberries (pedicels unjointed) to *Grossularia* is largely artificial, since other characters are incompletely correlated with the type of pedicel, and the gooseberries are now generally included in *Ribes* as subg. GROSSULARIA (P. Miller) Pers.[5] Five additional subgenera and numerous sections, some based on segregate genera proposed by Spach and sections established by Berlandier, were recognized by Janczewski (1907) in the only monograph to date that considers the genus on a world-wide basis. The more recent treatments by Coville & Britton (1908), Berger (1924), and Rehder (1940) have either treated the species in groups of undesignated rank or have been synthetic, inasmuch as the older infrageneric classification has been maintained, although species have been realigned and subgeneric taxa have been merged and redefined. As a result, subgeneric classification, nomenclature, and synonymy are confusing, and the genus is in need of a thorough taxonomic revision, including typification, with the application of current rules of nomenclature.

Although *Ribes* is ubiquitous in the North Temperate Zone, the greatest concentration of species occurs in North America, where over 70 species are indigenous. Seven species in two subgenera are native in the southeastern United States, but the bulk of the North American species, representing four subgenera, is centered in the western Cordillera, and over 40 species have been attributed to the Californian flora alone. Of the six recognized subgenera, two comprised of dioecious species do not occur in North America and may represent more recent diversifications in secondary evolutionary centers. The 30 species of subg. PARILLA Jancz. are restricted to the Andes of South America, whereas the 20 species of subg. BERISIA Spach occur throughout the mountainous regions of Eurasia.

Subgenus GROSSULARIA (P. Miller) Pers. (*Grossularia* P. Miller, pro gen.; sect. *Eugrossularia* Engler) includes five species in our area with small, 1–4-flowered pendulous racemes, unjointed pedicels, turbinate to tubular floral cups, nodal spines, and scarious bud scales. *Ribes cynosbati* L., $2n = 16$, an arching shrub with bristly ovaries, included stamens with glabrous filaments, and nodal spines sometimes absent, is a species of rich woods and heath balds from New Brunswick southward in the mountains to the Carolinas, Tennessee, Georgia, and Alabama. Of more restricted distribution, *R. curvatum* Small (*Grossularia curvata* (Small) Cov. & Britt., *G.*

[5] This combination is commonly attributed to A. Richard (Bot. Med. 2: 488. 1823), but Persoon (Synop. Pl. 1: 252. 1805) initially treated *Grossularia* as a subgenus of *Ribes*.

texensis Cov. & Berger), occurs on granitic soils from the Piedmont of Georgia to Louisiana and eastern Texas. It is closely allied to the restricted endemic *R. echinellum* (Cov.) Rehder (*Grossularia echinellum* Cov.), $2n = 16$, which also has exserted stamens with villous filaments (cf. FIG. 7, j). The ovaries of *Ribes curvatum*, however, are covered with sessile glands, while in *R. echinellum* the ovaries and fruits are densely covered with gland-tipped spines, and the mature fruits resemble cockleburs (*Xanthium*). First discovered in the region of Lake Miccosukee in Jefferson County, Florida, *R. echinellum* has also been found growing as an understory shrub along Steven's Creek in McCormick County, South Carolina, some 250 miles to the north-northeast.

The two additional species of subg. GROSSULARIA sect. EUGROSSULARIA in the Southeast have glabrous ovaries and purplish-brown fruits. Indigenous to the eastern United States from Massachusetts and New York southward through the mountains into North Carolina and Tennessee, *Ribes rotundifolium* Michx. occurs in rich woods and on grassy balds. It is closely related to the widespread Middle Western species, *R. missouriense* Nutt. ex Torrey & Gray (*Grossularia missouriensis* (Nutt.) Cov. & Britton, *R. gracile* Pursh), $2n = 16$, that occurs in moist to dryish upland woods from South Dakota and Kansas eastward to Minnesota and western Tennessee. Shrubs of both species often lack nodal spines, and the flowers have exserted stamens and nearly cylindric floral cups, but in *R. missouriense* the peduncles are commonly longer than the pedicels, and the style is 10–12 mm. long, while in *R. rotundifolium* the peduncles are usually shorter than the pedicels, and the styles are 6–8 mm. long.

Subgenus COREOSMA (Spach) Jancz. (included in subg. RIBES [subg. *Ribesia* Berl.] by Rehder) includes two spineless species of the Southeastern states with jointed pedicels and perfect flowers usually in several-flowered racemes. Section HERITIERA Jancz. is represented by *Ribes glandulosum* Grauer (*R. prostratum* L'Hérit.), $2n = 16$, a sprawling, prostrate shrub with erect or ascending racemes of eight to twelve flowers with hispid ovaries that are covered with crystalline glands. In fruit, the ripe ovaries become a bright red. Indigenous to boreal regions from Labrador and Newfoundland to the District of Mackenzie and British Columbia, it ranges southward to Minnesota, Michigan, New York, the New England States, and in the mountains into North Carolina and Tennessee where it grows at high elevations in *Picea-Abies* forests and on grassy balds. In boreal regions, however, the shrubs are usually found in swamps, bogs, and cold, wet, coniferous forests.

Ribes odoratum Wendl., $2n = 16$, included in sect. SYMPHOCALYX Berl. (sect. *Siphocalyx* Endl., *Chrysobotrya* Spach, pro gen.) with other species with yellow calyces and leaves convolute in bud, is an occasional escape from cultivation in eastern North America but is indigenous from Minnesota to Arkansas and west and south to South Dakota, Colorado, and Texas, where it grows on cliffs and rocky hillsides. Closely allied to and sometimes considered and treated as conspecific with *R. aureum* Pursh, of the western cordillera, *R. odoratum* is characterized by its frag-

rant flowers with tubular floral cups 11–15 mm. long, and globose, black berries.

The vegetative anatomy of *Ribes* has recently been reviewed and studied by Stearn *et al.* (1970), who concluded that the genus is remarkably homogeneous anatomically and that no consistent anatomical differences support the recognition of *Ribes* sensu stricto and *Grossularia*. As in several genera of the Saxifragoideae, leaves of *Ribes* are characterized by the presence of hydathodes along the blade margins. A trimerous vascular skeleton, originating from trilacunar nodes, and the presence of bulbous-based, unicellular hairs are also consistent features of the leaves. Stomata, of the ranunculaceous type, are restricted to the lower leaf epidermis in all but a few species, and cells adjacent to the guard cells cap their inner surfaces. Wood of *Ribes* is diffuse or ring-porous, and the small to extremely small vessels of all but two investigated species consistently possess scalariform perforation plates; in both *R. aureum* and *R. americanum* completely simple and simple plates with vestigial bars are also present. Intervascular pitting is scalariform to opposite, rarely alternate, and the pits are circular to elongate in outline. Rays, both homocellular and heterocellular, are of two distinct widths, and axial parenchyma is not present.

Flowers of *Ribes* vary considerably in the depth and shape of the floral cup extending beyond the inferior ovary, the length of the anther filaments, the relative length of the style, and the coloration of the calyx and corolla, apparently in adaptation to cross-pollination by insects, and in some species, possible self-pollination. Moreover, homogamy, proterogyny, and proterandry, in addition to dioecism, are biologic characters that have been observed or inferred and employed in the division of the genus into infrageneric taxa.

Initiation of flower and inflorescence primordia occurs under short-day conditions during the growing season preceding the year of anthesis, usually, after extension growth of the stem has ceased. Terminal buds remain vegetative, and inflorescences are produced in the axillary buds of the current year's shoot, or alternatively in "spur" shoots that are axillary branches of shoots two or more years old.

Anthesis occurs in spring, often before the foliage is fully matured, and both self-compatibility and self-incompatibility have been demonstrated for numerous species and horticultural varieties. Nectar production at the base of the floral cup is sometimes localized in an obvious disc, and ethereal oils secreted by epidermal glands on the calyx often make the flowers fragrant. Fly and bee pollination seems to be the general rule, but Grant & Grant have described "chin" pollination by hummingbirds of the pendulous, red flowers of *Ribes speciosum* that have elongated tubular floral cups. Coville (1924) described pollination of flowers of *R. echinellum* by carpenter bees and noted that the long hairs on the staminal filaments of that species enable the insects to alight and hold on as they probe for nectar in the pendulous flowers.

Although Hamel (1955) reported a chromosome number of $2n = 32$ for garden plants of the South American *Ribes Gayanum* (Spach) Steud., and

Russian investigators have reported tetraploid and triploid progeny in the F_1 generation of a red currant hybrid, polyploidy has not been an important evolutionary mechanism in the genus as is evidenced by the stability of the diploid number, $2n = 16$, reported for all other investigated species (96 to date). The chromosomes are small and do not differ significantly in morphology between species, and a pair of satellited chromosomes occurs consistently in the karyotypes of all species studied. Chromosomal fragmentation, translocation, and similar structural changes also appear to have been of little consequence in the genus, at least within sections since pairing during meiosis in numerous spontaneous and artificial hybrids is regular, univalents are rare, pollen abortion percentages are low, and numerous fertile seeds are produced. In sterile or only partially fertile hybrids, usually between species of different sections or subgenera, meiosis is disrupted by the presence of univalents, and allosyndetic pairing when it does occur is often hampered by differences in homologue length. Sterility and pairing difficulties are easily overcome, however, through treatment with colchicine, and numerous tetraploid hybrids, often of horticultural value, have been produced experimentally. Cytological studies of colchicine-induced tetraploids of *R. nigrum*, the black currant, have shown great variation in the number of chromosomes in somatic cells, and Vaarama (1948) has interpreted the presence of only four chromosomes in some somatic cells to indicate that extant diploids are derived tetraploids and that the original base number of the genus was four.

An embryological feature characteristic of the genus is the presence of apical "caps" on the hooked synergids, structures that have been reported elsewhere only for *Helianthemum vulgare* (Cistaceae) and *Sedum ternatum* (Crassulaceae).

Fruits of *Ribes* are eaten by mice and other small rodents, but the seeds are destroyed, while passage of seeds through the viscera of birds appears to speed germination, and species dispersal is probably largely by birds. In experimental studies, seed dormancy has been broken by stratification.

In our area, fruits of both *Ribes cynosbati* and *R. rotundifolium* were eaten by Indians, and gooseberry pie made from these fruits was famous in colonial times. Numerous cultivated varieties of *R. nigrum*, the black currants, *R. rubrum* sensu lato, the red currants, and *R. Grossularia*, the gooseberries, have largely replaced wild species as eatables, although they are grown commercially only on a small scale and are of minor economic importance. Several species, including *R. aureum* and *R. sanguineum*, are sometimes cultivated in gardens for their ornamental value, and shrubs of both ornamental and edible species often escape cultivation and persist in abandoned door yards.

Often associated during stages of secondary succession with the white pines of *Pinus* subg. *Strobus* Lemm. sect. *Quinquefoliis* Duhamel,[6] species

[6] See E. L. Little, Jr., & W. B. Critchfield, subdivisions of the genus *Pinus* (Pines). U.S. Dep. Agr. Forest Serv. Misc. Publ. **1144**. 51 pp. 1969.

of *Ribes* are the primary hosts of *Cronartium ribicola* J. R. Fischer, a long-cycled heteroecious rust and causative organism of pine blister, a disease that also affects five-needled pines. Basidiospores produced by promycelia of *C. ribicola* parasitic on the lower surfaces of the leaves of *Ribes* are capable of dispersal over relatively short distances to neighboring pines, but aeciospores produced in aecia on the pine host can be carried considerable distances to receptive *Ribes* populations. As a result, species of *Ribes* have been subject to programs of eradication throughout much of their range in North America and Europe as a disease control measure, particularly where the shrubs are coincident with commercially valuable pine forests.

Repeatedly introduced into New York State and New England from Europe at the turn of the century on inexpensive white pine nursery stock for reforestation programs, the rust had become widely distributed by 1920 throughout the northeastern United States. Although some workers have claimed that *Cronartium ribicola* was introduced into Europe on stock of *Ribes aureum*, it seems likely that the fungus was originally endemic on *Pinus cembra* in western Siberia and perhaps in the Swiss Alps. Although all of the five-needled pines are equally susceptible to the fungus that eventually causes the death of infected trees, different species and varieties of *Ribes* have been shown through artifical innoculations to differ considerably in their susceptibility. Snell reports that the economically and horticulturally important currants and gooseberries are sufficiently immune to the rust to eliminate the necessity of their eradication as a disease control measure.

As an amply distinct genus characterized by its woody habit, alternate and/or fasciculate leaves with palmate venation, inferior ovaries that develop into juicy or pulpy berries, and its distinctive, multiporate pollen morphology (Agababian, 1963), the affinities of *Ribes* within the Saxifragaceae sensu Engler are obscure. Engler (1891) originally placed the genus in its own subfamily, the Ribesioideae (the placement restored in the 1964 edition of the *Syllabus*), but in 1928 included *Ribes* in the tribe Ribesieae A. Rich. in the otherwise predominantly herbaceous subfamily Saxifragoideae. Others, convinced of its isolated position within the Saxifragaceae, have recognized the segregate family Grossulariaceae (DC. in Lam. & DC. Fl. Franç. ed. 3. **5**: 405. 1805, nom. cons.), but the placement of that family and its composition have remained problematic.

Cronquist placed the Grossulariaceae in his Rosales (in which he includes all of Engler's saxifragaceous taxa) but enlarged the family to include the woody, alternate-leaved genera that were treated by Engler as constituting the subfamilies Brexioideae, Escallonioideae, Montinioideae, Phyllonomoideae, Pterostemonoideae, Tetracarpaeoideae, and Iteoideae. Hutchinson (1959, 1967, 1969), by contrast, retained the Grossulariaceae as monogeneric but enlarged the Escalloniaceae to include (with the exception of the Pterostemonaceae) Engler's other subfamilies listed above, and placed these families in his Cunoniales. Takhtajan, on the other hand, treated each of the subfamilies as a segregate family and initially (1959) in-

cluded them in the Cunoniales but later (1969) reassigned them to the Saxifragales.

With the exception of *Itea* and five of the six subgenera of *Ribes*, the taxa aligned by Cronquist, Hutchinson, and Takhtajan are distributed primarily in tropical and subtropical regions of the Southern Hemisphere. As a group, Engler's subfamilies illustrate sometimes strong, sometimes weak reticulate relationships with one another, yet they are undoubtedly polyphyletic. New criteria are needed to resolve more clearly their relationships with one another and the Saxifragaceae sensu stricto.

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Subfam. ITEOIDEAE Engler

12. Itea Linnaeus, Sp. Pl. 1: 199. 1753; Gen. Pl. ed. 5. 92. 1754.

Erect, deciduous [or evergreen] shrubs [or small trees] with slender, virgate branches; pith terete, white, chambered; axillary buds superposed, with 3 or 4 overlapping scales; leaf scars elliptical to reniform with 3 prominent bundle scars. Leaves alternate, short petiolate, with 2 minute, simple, free, caducous stipules at base of petiole [or leaves apparently exstipulate]; blades simple, elliptic to obovate with an acute or short-acuminate apex and a cuneate base, glabrous above, finely pubescent below, the venation pinnate, the margins serrate, serrulate, [spinose, or dentate]; foliage (in ours) turning brilliant red in the fall. Flowers perfect, in many-flowered, often elongate [axillary or] terminal racemes that (in ours) become secund in fruit, the pedicels short, each with a membranaceous, subulate bract and 2 lateral stipules on abaxial surface near its articulation with

rachis, both bracts and stipules caducous. Calyx of 5 erect sepals united below into a shallowly obconic [or campanulate] floral cup; calyx lobes subulate [or ovate], persistent. Corolla white to pinkish, the petals 5, linear, with incurved apices, valvate in bud, inserted on inner surface of rim of floral cup, suberect, but spreading during anthesis. Stamens 5, inserted opposite calyx lobes at outer edge of an annular to slightly lobed

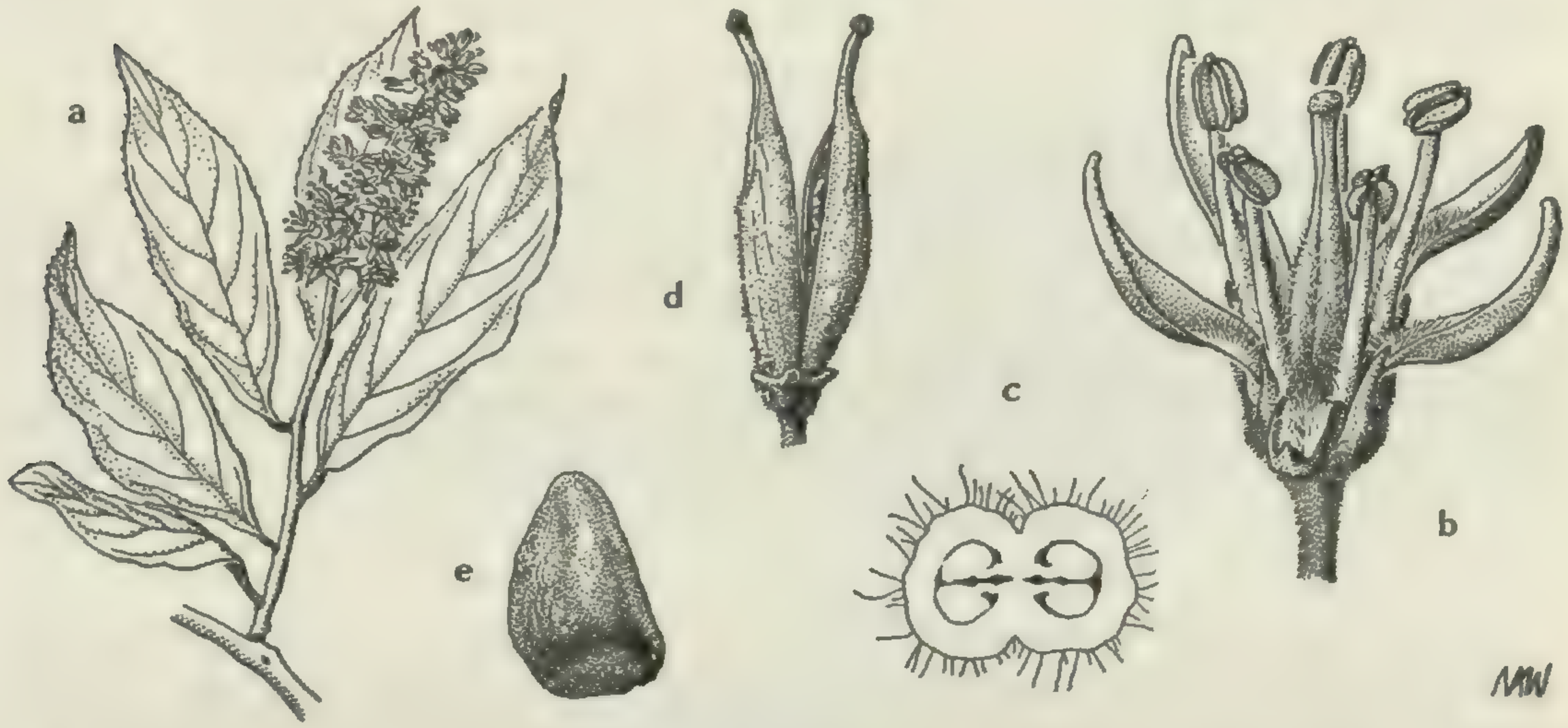

FIGURE 8. **Itea**. a–e, *I. virginica*: a, habit of flowering branch, × 1/2; b, flower, showing petals with incurved apices and confluent styles, × 5; c, cross section of two-loculate ovary with ovules biseriate on axile placentae, × 15; d, two-beaked, two-valved septicidal capsule, × 3; e, seed, × 15.

disc at base of floral cup; filaments tapering gradually to the oblong, 2-loculate, yellow anthers that dehisce introrsely by longitudinal slits; pollen subisopolar, bilateral, and 2-porate, the apertures ± circular to lolongate. Gynoecium 2-carpellate, the carpels connate below, incompletely connate above; styles 2, confluent and seemingly 1, becoming bipartite in fruit; stigmas capitate; ovary superior [or partially adnate to the floral cup below], pubescent, 2-loculate, with the numerous anatropous, crassinucellar, bitegmic ovules 2-seriate on axile placentae. Fruit a septicidally 2-valved, 2-beaked capsule, dehiscing between the styles. Seeds numerous, oblong to ovoid and irregularly compressed [or elongate and narrowly fusiform], the surface black and shining; embryo straight, relatively large; endosperm scanty. Base chromosome number 11. (Including *Diconangia* Adanson, *Kurrimia* Wall. ex Meisner, *Reinia* Franchet.) TYPE SPECIES: *I. virginica* L. (*Itea*, the Greek name of the willow, *Salix*, in allusion to the catkin-like appearance of the racemes of white flowers, or perhaps to the willow-like foliage.) — VIRGINIA WILLOW, SWEET-SPIRE, TASSEL-WHITE.

A well-marked genus of perhaps ten or eleven species restricted to eastern North America and eastern Asia, one in the eastern United States and about ten distributed from the northwestern Himalayas to Taiwan and

Japan southward into tropical regions in eastern India, Java, and the Philippines. One of the woody genera that allies the floras of eastern Asia and eastern North America, *Itea* formerly had a wider distribution and probably ranks as a Tertiary relict. Fossil pollen of one or perhaps two species has been detected in early and middle Miocene deposits from the Pacific Northwest and Alaska (Wolfe, 1970) and Takhtajan (1969) cites investigations that have referred macrofossils from the Baltic ambers to the genus.

Itea virginica L., $2n = 22$, of our area and the closely allied *I. japonica* Oliver, endemic to middle Japan, which constitute section ITEA (§ *Deciduae* Engler), are deciduous plants with oblong to ovoid seeds in this genus of predominantly evergreen species. The remaining species, all of which are warm-temperate and evergreen, have fusiform seeds, and are Asiatic, comprise sect. SEMPERVIRENTES Engler.

In eastern North America, *Itea virginica* occurs over a wide area from southern New Jersey and eastern Pennsylvania southward to Broward County, Florida, and west to southern Illinois and eastern Missouri, Oklahoma, and Texas. Although known from a few scattered localities in the mountains of Tennessee and western North Carolina, *I. virginica* is primarily a species of the Coastal Plain, adjacent Piedmont, and the Mississippi Embayment in our area, and indirect evidence from Pleistocene sediments in Georgia (Watts, 1970) suggests that the present "Coastal Plain disjunct" distribution pattern has been attained during postglacial time. Usually occupying moist or wet sites, where the shrubs may become arborescent and up to three meters high, *I. virginica* is most common in swamp forests and low woodlands; when it occurs in upland areas it usually grows along sandy creek and river banks and pond margins.

The only woody saxifragaceous species in North America with alternate, stipulate leaves, *Itea virginica* can be readily identified during winter months by its superposed axillary buds and chambered pith. Anthesis occurs in late spring and early summer. The inflorescences usually are 3–17 cm. long, but Fernald (1947) described shrubs from southeastern Virginia with extremely short racemes (1–2.2 cm. long) as forma *abbreviata*.

Although the pollination ecology of *Itea* has not been studied closely, it is evident from an examination of flowers of *I. virginica* that the anthers dehisce soon after the flowers have opened while the stamens are stiffly erect and the anthers are positioned directly over the stigmas. With age, the stamens and petals gradually move downward, and the capitate stigmas are exposed. Chromosome studies of five species (*I. virginica*, *I. parviflora* Hemsley, *I. chinensis* Hooker & Arn., *I. macrophylla* Wall., and *I. ilicifolia* Oliver) suggest that the genus is probably homogeneous cytologically, since $2n = 22$ has been reported for each of these species. Compatibility relationships and breeding mechanisms have not been investigated.

Generic relationships and the position of *Itea* have been problematic, since the genus is distinctive in several features yet appears to have affini-

ties with both the Saxifragoideae and the Escallonioideae. Engler (1891) originally included *Itea* in the Escallonioideae but later (1928) removed it to its own subfamily, the Iteoideae, while Hutchinson (1959, 1967) retained *Itea* in the woody escalloniaceous group but elevated that group to the rank of family. Britton (1905) and Takhtajan (1959) considered *Itea* distinctive enough to merit segregation at the familial level, and resurrected the Iteaceae, nom. cons., originally established by J. G. Agardh (1858). Cronquist (1968), on the other hand, included *Itea* in his broad circumscription of the Grossulariaceae (cf. *Ribes*).

The distinctive and exceedingly uncommon pollen morphology (bilateral, 2-porate) found in *Itea* has been one of the primary arguments used to justify recognition of the Iteaceae (see Agababian, 1960, 1961, 1964; Takhtajan, 1959) and has also reaffirmed the relationship alluded to by Bentham & Hooker between *Itea* and *Choristylis* Harv., a genus of one or two species that also exhibits "iteoid" pollen.[7] Restricted to East Tropical and South Africa, *Choristylis* has been placed in the Escallonioideae near *Forgesia* Comm. ex Juss., from Réunion, but is now generally placed with *Itea* (see Erdtman, 1956, 1969). Chemical data (Jay, 1971) suggest that the affinities of *Itea* may be with *Brexia* Noronha ex Thouars, another East African genus isolated within the Escallonioideae that has, at times, been segregated into its own monogeneric family.

Itea differs from genera of the Escallonioideae in its distinctive chambered pith, stipulate leaves, and confluent styles and stigmas. Moreover, Mauritzon (1933, 1939) has stressed that the bitegmic, crassinucellar ovules and the details of development and the structure of the embryo sac of *Itea* coincide most closely with the conditions met with in the Saxifragoideae, and he urges assignment of *Itea* either within or near that subfamily. The corresponding embryological characters in investigated escalloniaceous species indicate that typical ovules are unitegmic and tenuinucellate. Endosperm formation, nucellar in the Escallonioideae and cellular in the Saxifragoideae, has not been described for *Itea*.

The wood of *Itea* is diffuse-porous, averaging about 20 vessel elements per square millimeter, and the vessel perforation plates are scalariform, each with 40–70 delicate bars. In escalloniaceous genera intervascular pits are round and usually opposite, and pits to the ray and wood parenchyma are small and round, while in *Itea* intervascular pitting is scalariform, and the pits to ray and wood parenchyma are large and oblong.

Itea ilicifolia, of central and western China, and *I. yunnanensis* Franchet, of Yunnan, are occasionally cultivated as garden ornamentals. Both evergreen shrubs with holly-like leaves, these two species are probably less hardy in northern gardens than *I. virginica*, which is especially attractive in the fall when its foliage turns a brilliant red.

[7] Pollen closely resembling "iteoid" pollen has been described and figured for two saprophytic herbaceous genera of the Gentianaceae, *Leiphaimos* and *Voyria* (S. Nilsson & J. J. Skvarla. Pollen morphology of saprophytic taxa in the Gentianaceae. Ann. Missouri Bot. Gard. **56**: 420–438. 1969).

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Subfam. HYDRANGEOIDEAE A. Br.

Tribe PHILADELPHEAE Reichenb.

13. **Philadelphus** Linnaeus, Sp. Pl. 1: 470. 1753; Gen. Pl. ed. 5. 211. 1754.

Much branched, erect, arching [or subscandent], deciduous shrubs up to 5 m. high, often planted for their showy, often fragrant flowers. Branches opposite, terete or finely ridged, the cortex and periderm tight and persistent or flaking or exfoliating in thin strips, the periderm on

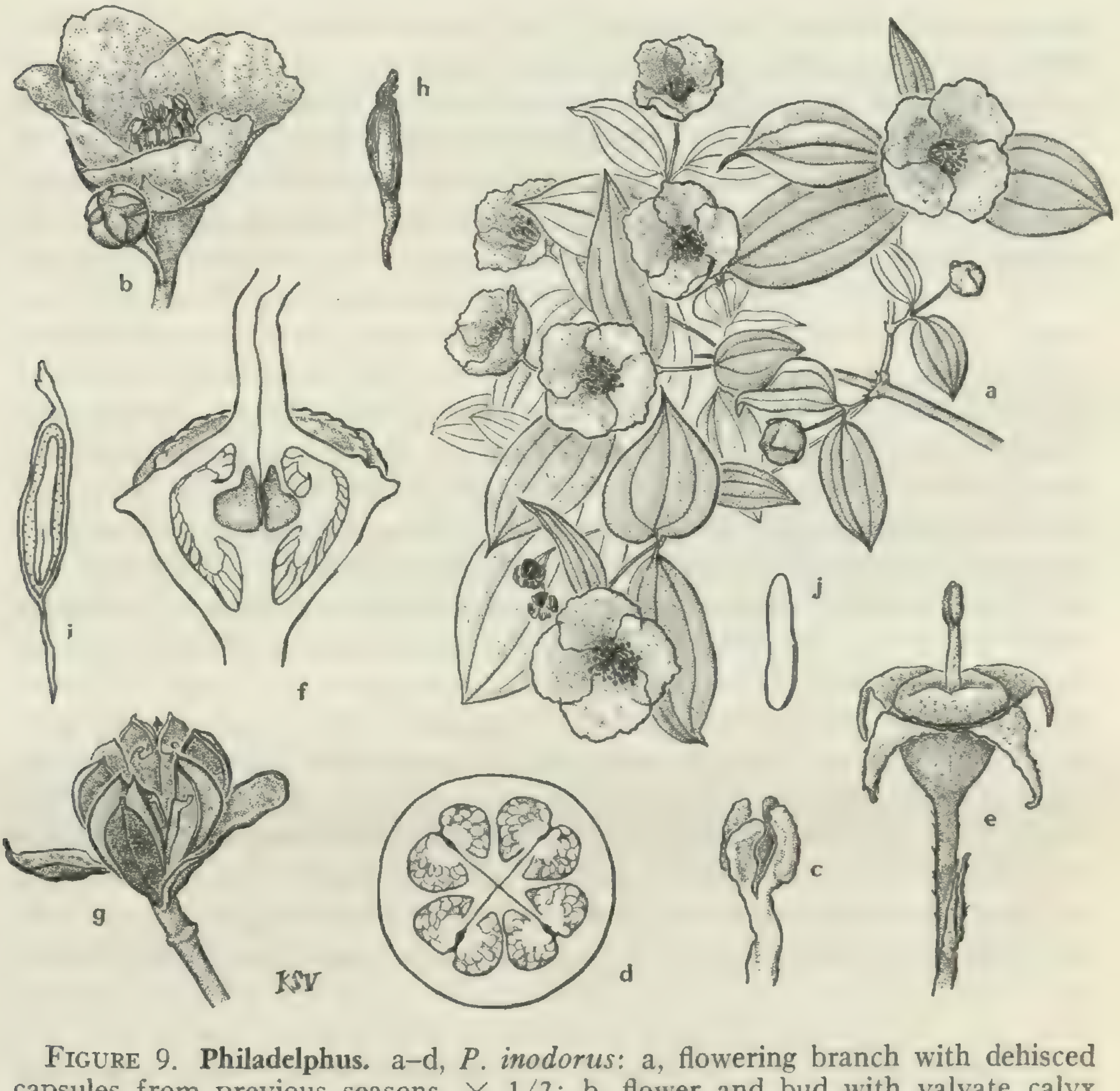

FIGURE 9. **Philadelphus.** a–d, *P. inodorus*: a, flowering branch with dehisced capsules from previous seasons, × 1/2; b, flower and bud with valvate calyx lobes, × 1; c, detail of style and four-lobed stigma, × 6; d, cross section of ovary, × 5. e–i, *P. hirsutus*: e, immature fruit soon after disarticulation of corolla and androecium — note undivided stigma and ovarian disc, × 3; f, vertical section through immature fruit showing auriculate placentae and pendulous ovules, × 5; g, mature, dehisced capsule, × 2; h, seed, × 6; i, longitudinal section of seed showing embryo, × 12; j, embryo oriented as in seed, × 12.

older shoots gray, grayish-brown, or reddish, the epidermis on new growth greenish or chestnut-brown; pith spongy and pale white, terete; lateral buds solitary with 2 valvate scales [or several imbricate scales]; leaf scars elliptic or cordate, transversely connected, with 3 bundle scars. Leaves short-petiolate, exstipulate; blades dark green above, pale green below, glabrous or variously pubescent, lanceolate, elliptic, or ovate in outline, with acuminate apices and attenuate, obtuse, or truncate bases; margins entire or irregularly serrate or dentate (the apiculate teeth seemingly associated with hydathode-like vein endings); venation pinnate with 3 or 5 major nearly parallel veins. Flowers short-pedicellate, usually with 2 erect, linear bracts subtending the flower; flowers borne singly or in 2's or 3's (a simple dichasium) at the ends of lateral branches, sometimes with paired

flowers at successively lower nodes, often in the axils of leaves. Sepals 4, rarely 5, connate below and adnate to the ovary, forming a turbinate to subcampanulate floral cup; calyx lobes valvate in bud, deltoid, with acute or acuminate apices, often becoming reflexed in fruit but deciduous before capsule dehiscence. Petals 4, rarely 5, imbricate in bud, inserted on rim of floral cup, white or rarely purplish, orbicular, ovate, oblong, or spatulate in outline, forming a disciform or cruciform corolla. Stamens numerous, usually erect and surrounding the style, inserted on rim of floral cup; filaments subulate, tapering gradually to the basifixed oblong or subglobose anthers, the anthers with obvious connectives; pollen (of 1 examined species) finely reticulate, 3-colpor(oid)ate (longicolpate), subprolate. Gynoecium 4(5)-carpellate, styles 4 (rarely 3 or 5), completely connate, partially free above [or in some cultivated forms completely free], terminated by free clavate, linear, or cristate stigmas, or stigmas connate and columnar or subcapitate; ovary semi-inferior or inferior, adnate to floral cup, 4(5)-loculate, with numerous tenuinucellar, anatropous, unitegmic ovules pendulous on auriculate axile placentae, the placentae projecting from the upper or middle portions of the central axis. Fruit a corticate, loculicidal capsule; seeds numerous, oblong-cylindric, with a membranaceous brownish or blackish testa, usually prolonged into a tail; embryo small, straight, embedded in fleshy, oily endosperm of the *ab initio* Cellular type. Base chromosome number 13. (*Syringa* Adanson non L.) LECTOTYPE SPECIES: *P. coronarius* L.; see P. A. Rydberg, N. Am. Fl. 22: 162. 1905. (Name commemorating Ptolemy Philadelphus, King of Egypt, 283–247 B.C., sometimes translated as brotherly love.) — MOCK-ORANGE, SYRINGA.

A taxonomically complex genus comprised of perhaps as many as seventy species in four subgenera exhibiting a disrupted arcto-Tertiary distribution in the North Temperate Zone and extending southward into Central America. Hu (1954, 1955, 1956) has recognized seven species representing two subgenera in the southeastern United States, and 39 species ranging in the Cordillera of western North America and extending southward through Mexico and into Panama. In Asia, 22 species are recorded as native from Korea, northeastern China, and Japan southwestward through China and into the Himalayan region, while three species are indigenous to southeastern Europe and Asia Minor.

According to Hu's treatment of the genus, subg. PHILADELPHUS (subg. *Euphiladelphus* Hu) (shrubs with enclosed lateral buds, determinate branching, and determinate racemose or few-flowered inflorescences comprised of flowers with 25–90 stamens, clavate or linear stigmas, and caudate seeds) includes five species in our area. Three, *P. intectus* Beadle, $2n = 26$, *P. pubescens* Loisel., $2n = 26$, and *P. Gattingeri* Hu, are stiff-branched shrubs with determinate racemes of flowers with ovate calyx lobes and medianly attached placentae, ellipsoid capsules with subapical, persistent calyx lobes, and short-caudate seeds. *Philadelphus intectus* (incl. var. *pubigens* Hu), up to 5 meters high, is characterized by its non-

exfoliating bark and inflorescences of five, seven, or nine flowers with disciform corollas and glabrous floral cups. Growing on steep, rocky bluffs and bluff tops, *P. intectus* is known from a few localities along the Cumberland River in north-central Tennessee and southwestern Kentucky and more commonly in north- and west-central Arkansas and eastern Oklahoma. According to Hu, the glabrous leaves and floral cups of *P. intectus* suggest a close relationship with *P. Lewisii* Pursh, of the Pacific Northwest, while in habit and leaf shape, it resembles *P. pubescens*.

Philadelphus pubescens (incl. var. *verrucosus* (Schrader) Hu; *P. latifolius* Schrader) is not only similar in habit to *P. intectus*, but it occurs in the same geographic areas, *viz.*, the Nashville Basin and the Ozark Plateau and Ouachita Mountains in Arkansas and eastern Oklahoma. It also occurs disjunctly in northeastern Texas, in Pope County, Illinois, and in McDonald County in southwestern Missouri. Apparently a calciphile of steep, wooded slopes, the plant is characterized by its pubescent foliage and seven- to nine-flowered inflorescences, the flowers with strigose-villose floral cups and cruciform corollas of glabrous, obovate-oblong petals. *Philadelphus Gattingeri*, known only from the type locality on the bluffs along the Cumberland River near Nashville, Tennessee, is doubtfully distinct from *P. pubescens*, but Hu has separated it on the basis of the pubescent abaxial surface of the petals, ovarian discs, and styles.

Both *Philadelphus floridus* Beadle, $2n = 26$, and *P. inodorus* L. (including vars. *grandiflorus* (Willd.) Gray, *laxus* Hu, *carolinus* Hu, and *strigosus* Beadle; *P. grandiflorus* Willd., *P. gloriosus* Beadle), $2n = 26$, are arching shrubs one to three meters high, with solitary flowers or true dichasia of flowers with long-acuminate calyx lobes, apically attached placentae, ellipsoid or subovoid capsules with median, persistent calyx lobes, and long-caudate seeds. Highly variable in leaf shape, corolla form (cruciform, disciform, and intermediate types are known), and pubescence, *P. inodorus* has glabrous pedicels and floral cups, while *P. floridus* has pubescent ones. *Philadelphus floridus* is known in nature only from the type locality on the rocky slopes of the Coosa River in Floyd County, Georgia. *Philadelphus inodorus* occurs on rocky slopes in rich, moist woodlands in the Piedmont and in the mountains from southwestern Virginia through the Carolinas and into Georgia and Alabama (where it extends southward onto the Gulf Coastal Plain) and westward into central Tennessee. Localities in northern Virginia, northern Kentucky, and Pennsylvania are probably based on plants that have escaped from cultivation.

Subgenus DEUTZIOIDES Hu (shrubs with exposed lateral and terminal buds, indeterminate branching, and solitary flowers or ternate inflorescences composed of flowers with 13–35 stamens, columnar or subcapitate four-grooved stigmas, and tailless seeds) includes one or possibly two species in the Southeast. *Philadelphus hirsutus* Nuttall (incl. vars. *intermedius* Hu and *nanus* Hu), $2n = 26$, a low, spreading shrub up to two meters high, is a plant of rocky ledges and bluffs in the mountains of southwestern North Carolina, northern Georgia and Alabama, and Tennessee, and it occurs disjunctly on the Ozark Plateau in north-central Arkansas.

It is characterized by flowers with pubescent floral cups, disciform corollas of ovate or suborbicular petals, and pubescent foliage. *Philadelphus Sharpianus* Hu (including var. *parviflorus* Hu) differs only in its glabrous floral cups, cruciform corollas of oblong petals, and sometimes glabrous undersurface of the leaves. *Philadelphus Sharpianus* is known only from a very local area in the Great Smoky Mountains in Tennessee and, like *P. hirsutus*, from a disjunct station in Van Buren County, Arkansas.

Although the genus is relatively well defined, Hu's hierarchy of subgeneric categories (including subgenera, sections, and series), which is based on the older, partial classifications of Koehne (1893, 1896, 1904) and Rehder (1940, 1949), needs a thorough review both to determine its biological validity and to bring the nomenclature into accord with the current Code. The apparent confusion that exists in intrageneric classification is largely due to the species problem in *Philadelphus*. Most species exhibit considerable morphological variation and consist of polymorphic population systems; determinations consequently are difficult. A plethora of specific and varietal names attests to attempts to recognize this variation, and the problem has been compounded by the description of many taxa from cultivation.

All of the investigated species of *Philadelphus* (35 to date) are diploids with $2n = 26$. Interspecific hybridization apparently occurs easily in horticultural collections, suggesting the possibility of hybridization in nature as well. Several hybrids of horticultural origin have been studied cytologically by Bangham (1929) and Janaki Ammal (1951) with differing results. Although Bangham reported no obvious meiotic disruptions in microsporogenesis in hybrids, Janaki Ammal noted chromosomal lagging and other abnormalities that often resulted in high percentages of abortive pollen. Bangham recorded $2n = 26$ for all the hybrids he studied, but Janaki Ammal found two triploid ($2n = 39$) cultivars of the trihybrid *P.* × *purpureo-maculatus* Lemoine and an aneuploid cultivar, *P.* 'Beauclerk' with $2n = 28$. Additional aneuploid counts from the progeny of triploid cultivars have been reported by Sampson (1955).

Anthesis occurs during May and June, and the odor of flowers of numerous species is suggestive of the fragrance of orange blossoms. Pollination is by numerous long- and short-tongued bees, dipterans, and lepidopterans that probe between the stamens for the abundant nectar secreted by the ovarian disc. *Philadelphus coronarius* L. has been observed to be protogynous, but self-pollination is undoubtedly possible once the anthers (which mature centripetally) begin to dehisce. Compatibility relationships, however, have not been investigated, and the maturation sequences in flowers of other species have not been observed. The petals and stamens are deciduous, but the styles persist for a longer period on the immature fruits, which gradually develop into woody capsules late in the growing season. The capsules remain on the shrubs for a considerable period before dehiscing, and the seeds may not be liberated until the following growing season. Dispersal of the ripe seeds is undoubtedly by wind.

Ovules of *Philadelphus* are unitegmic, anatropous, and tenuinucellar, and

the archesporal cell undergoes meiosis directly to form a linear tetrad of megaspores. The chalazal megaspore develops into a Polygonum-type embryo sac that, during development, becomes partially extra-ovular by passing through the micropyle. An endothelium forms around the lower half of the embryo sac, and a micropylar haustorium of two or four elongated cells develops.

Wood of *Philadelphus* is ring- or semiring-porous, typically with solitary vessels and paratracheal scanty parenchyma. Vessel perforation plates are scalariform or occasionally simple, and intervascular pits are small, round, and opposite. Stomata, of the ranunculaceous type, occur in foliage epidermis, and the leaf teeth are glandular in certain species with dentate or serrate leaf margins. Typically, a single cell layer comprises the palisade mesophyll, and in transverse sections the petioles disclose an open, crescent-shaped vascular bundle.

Initially placed in the Myrtaceae by A. L. de Jussieu, *Philadelphus* has not been allied with that family since D. Don (1826) established the Philadelphaceae. De Candolle, Endlicher, and Lindley recognized the Philadelphaceae as distinct but enlarged it to include *Decumaria* and *Deutzia* Thunb., a genus of about 40 species indigenous to south-central and eastern Asia. The affinities of *Philadelphus* with *Hydrangea* were alluded to by De Candolle, but Reichenbach (1828) was the first to include the above genera, along with *Hydrangea*, with other genera customarily included in the Saxifragaceae sensu lato. Together, *Philadelphus*, *Deutzia*, and several western North American genera (including *Neodeutzia* Small, *Fendlera* Engelm. & Gray, *Carpenteria* Torrey, *Jamesia* Torrey & Gray, *Fendlerella* Heller, and *Whipplea* Torrey) form a seemingly natural group, the tribe Philadelpheae Reichenb. of subfamily Hydrangeoideae in Engler's system. As delimited by Engler, the tribe is usually included in the Hydrangeaceae [8] when that family is segregated from the Saxifragaceae. The recent systems of Cronquist and Takhtajan (1966, 1969) both include the Philadelpheae in the Hydrangeaceae, but Hutchinson (1959, 1967) has distributed the genera of Engler's Hydrangeoideae rather indiscriminately between the Hydrangeaceae and Philadelphaceae.

Within the Philadelpheae, *Philadelphus* is morphologically most similar to *Deutzia* (a cytologically variable genus with recorded counts of $2n =$ 26, 78, 104, 127, and 130), *Fendlera* ($2n = 22$), a small genus of four xerophytic species in the southwestern United States and Mexico, and *Neodeutzia*, a genus of two species of northwestern Mexico which are often included in *Deutzia*. Differentiation between these genera, all comprised of shrubs, is based primarily on constant stamen numbers (*Deutzia*, *Fendlera*) or variable ones (*Philadelphus*, *Neodeutzia*), on modifications in stamen morphology, and on the numbers of parts comprising the calyx and corolla. Evidence from flavonoid chemistry (Jay, 1971) suggests that

[8] Hydrangeaceae Dumort. (Anal. Fam. 36, 38. 1829), nom. cons., and not Philadelphaceae D. Don (Edinb. New Phil. Jour. 1: 132–135. 1826), is used when *Philadelphus* is included with *Hydrangea* in a segregate family. See Appendix II, Int. Code Bot. Nomencl. 1972.

Deutzia is relatively unadvanced, while *Philadelphus* has attained greater chemical complexity, similar to that evident in *Hydrangea*.

Disease-free, easily grown, and readily propagated from cuttings, species of *Philadelphus* have been widely planted in the North Temperate Zone as late-spring to summer-blooming ornamentals. About fifty species and varieties and numerous interspecific hybrids of horticultural value, produced mainly by the Lemoine & Son Nursery in Nancy, France, are in cultivation. *Philadelphus coronarius* L., native to southeastern Europe and the Caucasus and one of the most widely cultivated species, may persist in old gardens and door yards. This species has also been used as parental stock for many of the hybrids available today. Aside from their horticultural value, species of *Philadelphus* are of no other economic importance, although water scented with the flowers was used as a perfume by the ancient Parthians.

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Tribe Hydrangeeae DC.

14. **Hydrangea** Linnaeus, Sp. Pl. 1: 397. 1753; Gen. Pl. ed. 5. 189. 1754.

Erect or ascending deciduous [or evergreen] shrubs or [small trees or high-climbing vines clinging by adventitious aërial roots]. Stems with reddish-brown exfoliating epidermis on new growth and dark grayish-black or brownish, sometimes exfoliating bark on older parts of shoots; pith round, relatively large, spongy and unlignified [or lignified]; lateral buds opposite and solitary, sessile or very short-stalked, globose-conical to oblong and spreading, with 4–6 exposed scales; leaf scars crescent-shaped or irregularly 3–5-angled with 3 bundle scars; nodes trilacunar. Leaves opposite [or rarely whorled with 3 at a node], petiolate; blades thin and membranaceous [or coriaceous in evergreen species], variously pubescent [or glabrous], ovate, lanceolate, or elliptic in outline, rarely deeply 4–6-lobed, with [entire] denticulate, or serrate margins, acuminate, acute or attenuate apices, and [attenuate, obtuse, or] truncate bases; venation reticulate, usually with a prominent midvein. Inflorescence a terminal (occasionally axillary) compound cyme or pyramidal thyrse [often appearing umbellate in evergreen species]; pedicels with numerous small, lanceo-

late bracts [or lacking bracts within the inflorescence, but the entire inflorescence inclosed in bud by several large, ovate, caducous bracts that leave distinct scars]. Flowers either fertile or neuter and inflorescences comprised of one or both types; neuter flowers lacking or present and terminating the branches in mixed inflorescences, or comprising entire inflorescences (particularly in cultivated forms), consisting of 3–5 enlarged, petaloid, white [through pink to blue] persistent calyx lobes, often with an obvious "eye" (comprised of abortive floral parts and sometimes normal-appearing stamens); fertile flowers (rarely lacking) central to the neuter flowers or comprising entire inflorescences, perfect [or imperfect by abortion, and the plants functionally dioecious]. Calyx of fertile flowers of 4 or 5 sepals, connate and adnate to the ovary, forming a ribbed, campanulate, hemispherical, or oblong patelliform floral cup with 4 or 5 persistent, deltoid calyx lobes projecting above. Petals 4 or 5 white, ovate or spatulate, inserted on the rim of the floral cup, valvate in bud and deciduous during anthesis [or rarely falling together as a calyptra at the onset of anthesis]. Stamens 8–10 [rarely to 20], inserted on the rim of the floral cup; filaments filiform and often contorted, tapering to the suborbicular to oblong, tetrasporangiate anthers. Gynoecium 2–4(5)-loculate, the ovary adnate to the floral cup, inferior [or half-superior] with numerous unitegmic, tenuinucellar, anatropous ovules on 2–4(5) axile placentae; styles 2–4(5), free (when the ovary is inferior) [or united at the base] and projecting from the center of a flat [or conical] ovarian disc; stigmas 2-lipped, crescent-shaped, at the apices of the styles. Fruit a brown, strongly ribbed, poricidal capsule, dehiscing between the styles; seeds numerous and small, linearly elliptic [or rarely circular and winged or sometimes caudate]; embryo small, linear, embedded in endosperm of the *ab initio* Cellular type. Base chromosome number 16. (*Hortensia* Commerson ex Jussieu, *Cornidia* Ruiz & Pavón, *Sarcostyles* Presl ex Seringe.) TYPE SPECIES: *H. arborescens* L. (Name from Greek, *hydor*, water, and *angeion*, the diminutive of *angos*, a vessel or container, in allusion to the shape of the mature, dehisced capsules.) — GRAYBEARD, SEVENBARK, HORTENSIA.

Twenty-four or twenty-five species customarily placed in two or three sections distributed in temperate and subtropical regions of eastern Asia, eastern North America, Mexico, Central and South America. In the Northern Hemisphere, the distribution of *Hydrangea* is that of a Tertiary relict with species in eastern Asia and eastern North America. The genus is also known from several Tertiary floras in China and western North America (including sites in Colorado, Idaho, California, Oregon, Washington, and Alaska), but fossil or extant species are not known from southeastern Europe and Asia Minor. Nine species of sect. HYDRANGEA (sect. *Euhydrangea* Maxim., subgen. *Hortensiella* Koehne, subgen. *Euhydrangea* (Maxim.) Schneider) are distributed from the eastern Himalayas to central and southern China, southward in the Malay Archipelago to Java, and in

the Philippines and Ryukyu Islands and Japan, while two species are native in eastern North America.

Endemic within our region, *Hydrangea quercifolia* Bartram, $2n = 36$, an arching or sprawling shrub up to 4 m. high characterized by pyramidal inflorescences, numerous large neuter flowers, and large, deeply four- or five-lobed leaves, occurs eastward from the Mississippi River in Louisiana, Mississippi, and southwestern Tennessee through south-central Tennessee and Alabama and into western Georgia and the panhandle of Florida. Occasionally forming dense thickets along stream banks, the shrubs occur in wet, sandy soils and on the slopes of deep ravines and canyons in deciduous forests. Hardy and cultivated northward, plants of *H. quercifolia* are infrequent escapes or persistent relicts in abandoned dooryards in the Mid- and North-Atlantic states.

Hydrangea arborescens L.,[9] $2n = 36$, an ascending shrub up to three meters high, commonly with numerous branches from the base, ovate to elliptic leaves with acute or acuminate apices, serrate margins, and the inflorescences broadly convex compound cymes, is widely distributed in eastern North America, ranging from southern New York to Georgia and Alabama and westward into Illinois, Missouri, and eastern Oklahoma. In contrast to *H. quercifolia*, a relatively invariable species, *H. arborescens* is polymorphic, especially in the presence or absence of neuter flowers and in leaf shape, size, and vesture. Up to eight additional taxa in this complex have been attributed to eastern North America, but McClintock (1957a) has treated these as comprising three subspecies of *H. arborescens* differentiated on the basis of leaf indumentum and trichome type.

Hydrangea arborescens subsp. *arborescens* (*H. vulgaris* Michx., *H. arborescens* var. *australis* Harbison) occurs throughout the range of the species. In our area it is primarily a shrub of the Piedmont and mountains, although populations are known from a few scattered localities on the Coastal Plain in North Carolina, Georgia, Alabama, Mississippi, and Louisiana. Leaves of this subspecies are glabrous on the under surface or have scattered, smooth-walled hairs along the mid- and secondary veins. The lower leaf surfaces of subsp. *radiata* (Walter) McClintock (*H. radiata* Walter, *H. nivea* Michx., *H. cinerea* Small, in part), by contrast, are white or silvery with a dense, felt-like indumentum of smooth-walled, uniseriate trichomes; in addition, the neuter flowers of this subspecies are sometimes bluish-white. Endemic within our area, subsp. *radiata* is known from the mountains and adjacent Piedmont of southwestern North Carolina, adjacent South Carolina and Georgia, and southeastern Tennessee. Plants having lower leaf surfaces with a grayish pilose or tomentose ap-

[9] Species of *Hydrangea* are sometimes confused with species of *Viburnum* (Caprifoliaceae) with inflorescences including radiate marginal flowers, and Mackenzie (Torreya 27: 81–83. 1927) asserts that *V. alnifolium* Marsh, and *V. americanum* Miller are taxonomic synonyms of *Hydrangea arborescens*. For a further discussion of this situation, see footnote 3, pp. 42, 43 in I. K. Ferguson, The genera of the Caprifoliaceae in the Southeastern United States. Jour. Arnold Arb. 47: 33–59. 1966.

pearance imparted by uniseriate trichomes with the walls roughened by tubercles are referable to subsp. *discolor* (Seringe) McClintock (*H. arborescens* var. *Deamii* St. John, *H. Ashei* Harbison, *H. arborescens* var. *discolor* Seringe, *H. cinerea* Small, in part). Less restricted in range than subsp. *radiata*, subsp. *discolor* is known from scattered localities from the mountains of the Carolinas, Georgia, and northern Alabama northwestward through Tennessee and Kentucky and into southern Indiana, Illinois, Missouri, Arkansas, and eastern Oklahoma.

Like all species of *Hydrangea* outside of cultivation, *H. arborescens* is a woodland shrub, occupying mesic slopes and ledges in deciduous forests, but both it and *H. quercifolia* appear to be sun tolerant, and they often grow at forest margins and in open areas when under cultivation. Although the ranges of both *H. arborescens* subsp. *discolor* and subsp. *radiata* occur completely within the range of subsp. *arborescens*, shrubs with intermediate foliage vesture are infrequent and usually appear to be intermediates between subspp. *discolor* and *radiata*. At one locality in Transylvania County, North Carolina, McClintock (1957a) found all three subspecies growing within yards of one another along with several aberrant individuals. She concludes, however, that intermediates "have not caused the character of [subspecies] populations to change."

Hydrangea arborescens and *H. quercifolia* comprise subsect. AMERICANAE (Maxim.) Engler (shrubs with white flowers, inferior ovaries, truncate capsules, and the seeds not caudate), but overall morphological similarities between *H. quercifolia* and *H. sikokiana* Maxim., a shrub with deeply four- to six-lobed leaves endemic to Honshu and Kyushu, Japan, and between *H. arborescens* and *H. aspera* D. Don, a wide-ranging east Asian species polymorphic with respect to foliage and pubescence, suggest that the closest allies of our species are these Asian species and not one another. McClintock (1957a) has included both *H. aspera* and *H. sikokiana* in subsect. ASPERAE Rehder (a subsection differing from the AMERICANAE in flower-color range and caudate seeds), but Engler (1928) recognized the similarities between *H. quercifolia* and *H. sikokiana* and included the latter species in subsect. AMERICANAE.

Division of *Hydrangea* into sections is based primarily on habit, since floral, inflorescence, and seed criteria (employed in subsectional delimitation) are variable. Sectional boundaries, nevertheless, are indiscrete, suggesting a history of reticulate and/or convergent evolution within the genus. With the exception of *H. integrifolia* Hayata, indigenous to the Philippine Islands and Taiwan, species of sect. CORNIDIA (Ruiz & Pavón) Engler (evergreen vines, rarely erect shrubs, with broadly ovate bracts at the base of the inflorescence, inclosing the inflorescence in bud) are restricted to the New World. Two Mexican species have been recognized, but one or two additional species may remain undescribed from the state of Chiapas (Nevling & Gómez-Pompa, 1968). The eleven additional species in sect. CORNIDIA are distributed in mountainous regions of Guatemala, central Costa Rica, Panama, and at moderate elevations in the Andes from Colombia to central Chile and adjacent Argentina. That some

recognized species in this section may, however, actually represent either staminate or carpellate plants of functionally dioecious species has been pointed out by Nevling & Gómez-Pompa (1968).

Widespread in eastern Asia and sometimes cultivated in western gardens, *Hydrangea anomala* D. Don, a high-climbing woody vine with deciduous foliage and with the petals of the flowers united at their tips and falling together as a cap at anthesis, has sometimes been placed in its own monotypic section, CALYPTRANTHE Maxim. Alternatively, the species has been placed in subsect. CALYPTRANTHE (Maxim.) McClintock within sect. HYDRANGEA, a section that otherwise includes deciduous shrubs or small trees with flowers with petals free at their apices. With the exception of *H. involucrata* Siebold, endemic to Japan and Taiwan, all species of sect. HYDRANGEA, including *H. anomala*, are characterized by bracteate inflorescences that lack at the base the large bracts which are caducous before anthesis.

Diploid, $2n = 36$, and one tetraploid, $2n = 72$, chromosome numbers have been recorded for *Hydrangea*, and three of the four taxa in our region are diploids; only *H. arborescens* subsp. *discolor* remains uncounted. Cytological investigations have been limited to species of sect. HYDRANGEA, although low percentages of viable pollen noted by Nevling & Gómez-Pompa in some species of sect. CORNIDIA might indicate disrupted meiotic mechanisms in those species. It is probable, however, as these authors suggest, that those species with low pollen stainability are carpellate plants of functionally dioecious species.

Only one spontaneous interspecific hybrid in nature and two hybrids, both apparently inviable, arising in horticultural collections have been reported. Since most species bloom at the same time and occupy similar habitats, it appears that interspecific isolation is largely genetic. Anthesis occurs from about the end of June through August and into September, although the persistent, often colorful neuter flowers may give a false impression of the actual duration of anthesis. Observations have not been recorded, but it appears that our species are proterogynous and that pollination by a wide variety of insects, including long- and short-tongued bees, numerous dipterans, moths and butterflies, and beetles, is the rule.

Plateau (1898), in observations of insects visiting inflorescences of *Hydrangea macrophylla* (Thunberg) Seringe (as *H. opuloides*) noted that insects flew directly to and landed on the center fertile flowers, bypassing the showy peripheral flowers. Fruit-set in inflorescences of *H. arborescens* subsp. *arborescens* in the southern Appalachians is normally high despite the usual absence of neuter flowers.

The poricidal capsules ripen during the fall, but dehiscence and dispersal of the numerous seeds probably does not occur until sometime during late winter or early spring. Dispersal is undoubtedly by wind, and old inflorescences with dehisced capsules often remain on the plants for some time before the lignified tissues of the peduncles decay.

Wood of *Hydrangea* is ring- or semiring-porous with small, typically

solitary vessels. Perforation plates and intervascular pits are scalariform, and both uniseriate and multiseriate rays are present; tracheids are often in definite radial rows. The epidermis, which commonly exfoliates, often contains tannin bodies, and raphide sacs containing mucilage are common in most plant tissues, particularly the leaves. Cork cambium is formed in the outermost part of the cortex. Foliage stomata in some investigated species are paracytic, but Reyenga & Karstens determined that stomata occurring in the lower epidermis of the calyx lobes of neuter flowers of *H. macrophylla* are actinocytic. These workers have also described the disintegration of the calyx stomata (a phenomenon apparently previously undescribed) during the growth of the calyx lobes that accompanies a "greening" phase at the termination of anthesis. During the "greening" period, the calyx lobes lose their characteristic coloration and become a dull, drab greenish-brown.

Numerous species of *Hydrangea*, all in sect. HYDRANGEA and including both *H. quercifolia* and *H. arborescens* (particularly *H. arborescens* f. *grandiflora* Rehder, a form with all neuter flowers, originally found growing spontaneously in Ohio) are widely planted in temperate regions as ornamentals. Most of the forms in cultivation were introduced to European and American gardens from Asia where the shrubs have been favorites in Chinese and Japanese gardens for centuries. Haworth-Booth (1950), McClintock (1956b, 1957a & b), and Nevling (1964) have reviewed the available information concerning the origins, culture, and history of the ornamentals.

Hydrangea macrophylla is the much-planted garden shrub and the "Hortensia" of florists with large globose inflorescences of white to pink and red through blue and purple neuter flowers. This species is well known to gardeners as a plant that will change its flower color depending upon the pH of the soil in which it is grown. Chromatographic separations of sepal pigments have shown that in both red and blue forms of *H. macrophylla* the pigments are identical, *viz.* a diglycoside of delphinidin containing glucose and arabinose. Additional phenolic compounds identified from sepal extracts include neochlorogenic and chlorogenic acids, kaempferol-3-glucoside, kaempferol-3-galactoside, and a kaempferol triglycoside containing galactose, glucose, and xylose (Asen *et al.*, 1957). The color or shade of the stérile flowers is dependent upon the ability of the plant to absorb and accumulate aluminum, the concentration of anthocyanin present in the sepals, and the ratio of the anthocyanin to the kaempferol glycosides. Aluminum has a marked effect on delphinidin diglycoside and the kaempferol pigments, causing marked shifts of absorption spectra toward longer wave lengths with a resulting shift from red to blue (Asen & Siegelman, 1957). Although the availability of aluminum is correlated with soil pH, the relationship between soil chemistry and sterile flower color in *Hydrangea* must still be clarified.

Included within the Saxifragaceae in the tribe Hydrangeae DC., subfam. Hydrangeoideae A. Br. by Engler, *Hydrangea* and its allied genera have more commonly been segregated from the Saxifragaceae and treated as

comprising the Hydrangeaceae Dumort. The Hydrangeaceae itself is often further divided (essentially along Engler's tribal lines) into the Hydrangeaceae *sensu stricto* and the Philadelphaceae (cf. under *Philadelphus*). Within the Hydrangeoideae, *Hydrangea* seems to be most closely related to *Platycrater* Sieb. & Zucc., a monotypic Japanese genus that differs only in its greater number of stamens, and *Cardiandra* Sieb. & Zucc., an East Asian genus of about five herbaceous species with alternate leaves. In inflorescence, flower, and fruit characters *Cardiandra* and *Platycrater* are essentially identical, and their relationships with *Hydrangea* should be investigated.

The dried root of *Hydrangea arborescens* contains hydrangin, an alkaloid, and is used medicinally as a diaphoretic and diuretic. In Japan, the wood of *Hydrangea* has been used in carving various small objects, and a sweet beverage, amacha, is prepared from steamed and dried young leaves of *H. Thunbergii*. Several accounts of both human and livestock poisoning from leaves have been reported in our area.

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15. **Decumaria** Linnaeus, Sp. Pl. ed. 2. 2: 1663. 1763; Gen. Pl. ed. 6. 238. 1764.

Climbing or trailing woody vines with adventitious aërial roots and deciduous [or occasionally persistent] foliage. Stems with grayish or reddish-brown bark, terete or slightly ridged from the enlarged nodes; epidermis and cortex of young shoots exfoliating; pith round or polygonal in cross section, greenish white and spongy. Lateral buds sessile, small and solitary with densely hirsute, reddish-brown, indistinct scales; leaf scars opposite, transversely connected, V shaped to linearly elliptic, inclosing 3 conspicuous bundle scars. Leaves opposite (occasionally 3 leaves at a node on vegetative runners), petiolate, the petioles short with slightly winged, exstipulate bases; blades dark green and glossy, glabrous [or with scattered hairs] above, lighter in color and finely pubescent along the veins below; ovate, elliptic, obovate [or oblanceolate] in outline with entire, irregularly dentate, or irregularly lobed margins and acute [obtuse, or rounded] apices and cuneate, obtuse, or truncate bases; venation pinnate with a prominent midvein. Flowers perfect, faintly fragrant, arranged in compact [or loose and broad], convex, terminal, many-flowered corymbs; each flower of the corymb usually subtended by an inconspicuous, linear bract. Calyx of 7–10(–12) sepals, connate and adnate to the ovary, forming a strongly 7–10(–12)-ribbed floral cup (often with additional ribs observable) with 7–10(–12) deltoid calyx lobes projecting above and persistent in fruit. Corolla of 7–10(–12) creamy-white, sessile, lanceolate petals inserted on the rim of the floral cup, valvate in bud. Androecium of 20–30 stamens, inserted on the rim of the floral cup; filaments often contorted, subulate, tapering only slightly to the basifixed, suborbicular to ovate anthers, which have obvious connectives. Gynoecium 7–10(–12)-loculate, the ovary inferior, adnate to the floral cup, with numerous, tenu-

FIGURE 10. **Decumaria** and **Hydrangea.** a–i, *D. barbara*: a, shoot with terminal corymb, × 1/4; b, detail of flowers — note radiating stigmatic lines, × 3; c, detail of anther showing obvious connective, × 12; d, vertical section of flower (petals and anthers removed) showing stylar column and axile placentation, × 6; e, cross section of ovary, × 12; f, immature capsule with persistent style and stigma, × 5; g, completely dehisced capsule, × 5; h, seed, × 12; i, embryo oriented as in seed, × 25. j, *H. arborescens* subsp. *arborescens*: mature dehisced capsule, seen from above, × 10.

inucellar, anatropous ovules pendulous on axile placentae; style 1, thick and elongated [or very short and the stigma essentially sessile], projecting from the center of the ovarian disc and terminating in a knoblike, capitate stigma with 7–12 radiate stigmatic lines. Fruit a prominently ribbed capsule, terminated by the persistent stigma and dehiscing between the ribs (through the decay of the tissue); seeds small and numerous, the small cylindrical embryo surrounded by scanty endosperm of the *ab initio* Cellular type and a loose, membranaceous, lustrous yellow, often caudate seed coat. Base chromosome number 14. TYPE SPECIES: *D. barbara* L. (Name

from Latin, *decimarius*, relating to tenths, in reference to the usually ten-merous flowers.) — CLIMBING HYDRANGEA, WOOD-VAMP.

A genus of two recognized and perhaps one undescribed species of eastern Asia and eastern North America. *Decumaria barbara*,[10] $2n = 28$, a high-climbing or occasionally trailing vine with ovate to obovate leaves with acute apices, flowers in compact rounded terminal corymbs, and the gynoecia terminated by single, toplike styles with radiating stigmatic lines, occurs in rich deciduous forests and swamps from southeastern Virginia into Florida and westward to Louisiana and Tennessee. Essentially restricted to the Coastal Plain in Virginia and North Carolina, the species is more widely distributed in the southern part of its range, and it occurs at low elevations in mountain valleys in southwestern North Carolina, northern Georgia, and eastern Tennessee.

Adequately distinct from the American species, *Decumaria sinensis* Oliver is a low-climbing, often branched vine with semipersistent or persistent oblong leaves with obtuse or rounded apices; flowers in loose, open corymbs; and gynoecia with very short styles or completely sessile stigmas. Restricted to central China, *D. sinensis* apparently grows over a relatively narrow altitudinal range (1000–1300 meters) in the mountains of western Hupeh and eastern Szechuan. Variation within *D. sinensis* occurs in eastern Szechuan, and collections of plants with obviously persistent foliage and greenish flowers comprising small, tight corymbs may represent a third species.

A single chromosome count, $2n = 28$, has been recorded for *Decumaria barbara* by Sax (1931). No information concerning floral biology has been recorded, although the fragrance of the flowers probably attracts flying insects as pollinators. Depending upon geographic locality, anthesis occurs from April through June, and examination of preserved flowers suggests that they are either proterandrous or homogamous. The light weight of the caudate seeds and the climbing habit of the plant strongly suggest that dispersal is by air currents. Release of ripe seed probably occurs over a prolonged period (beginning in the fall) since decay of the intercostal tissue is slow, and the mature capsules and inflorescences remain on the vines through the winter.

Assignment of *Decumaria* to the tribe Hydrangeeae DC. in subfam. Hydrangeoideae is generally accepted, since the genera comprising the tribe appear to be closely allied. *Decumaria* shows strong affinities with *Schizophragma* Sieb. & Zucc. (two or three species of eastern Asia with reported chromosome numbers of $2n = 28$ and 72) and *Pileostegia* Hooker f. & Thomson (two species of eastern Asia), and generic lines merit re-evaluation. As in *Decumaria*, styles in flowers of both *Schizophragma* and *Pileostegia* are united and terminate in large, capitate stigmas, and the dehiscence of the ribbed capsules is effected by the decay of intercostal

[10] The specific epithet, *barbara*, is in reference to the Barbary Coast. The species was originally thought to be indigenous to Africa.

tissue. Members of all three genera are woody climbers with opposite leaves and paniculate or corymbose inflorescences, but in *Pileostegia* the foliage is consistently persistent, and the corolla consists of fused petals that form a caducous calyptra. In *Schizophragma*, unlike *Decumaria*, the androecium consists of only eight to ten stamens, and the corolla is composed of four or five petals. Although two species of *Schizophragma* have large, showy, neuter flowers with one greatly enlarged calyx lobe (cf. *Hydrangea* for discussion of neuter flowers), *S. crassum* Hand.-Mazz. lacks these and appears to link the genus closely with both *Decumaria* and *Pileostegia*.

Although both species of *Decumaria* have occasionally been grown as ornamentals in botanic gardens and arboreta, their use outside of warm-temperate regions is limited because of winter-tenderness and high water requirements. No economic or other uses have been reported.

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STUDIES ON BIGELOWIA (ASTERACEAE), II. XYLARY COMPARISONS, WOODINESS, AND PAEDOMORPHOSIS

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MAJOR TRENDS IN XYLEM evolution discovered through the efforts of I. W. Bailey and his contemporaries have become generally accepted (see Carlquist, 1961; Esau, 1965; Fahn, 1967, for review). The apparent universality of the xylem trends has been of great comfort to systematists in their application of anatomic data to phylogenetic considerations. However, the concepts were developed by comparative studies, particularly among the Dicotyledoneae, in which the secondary xylem of woody shrubs and trees was used almost exclusively. This basis may provide an incomplete, perhaps biased, view of xylem evolution, as suggested by Carlquist (1962) in his study of juvenility in rosette trees and woody herbs. He concluded that woods from such growth forms may not be comparable to those from woody shrubs and trees. His further studies (1969a, 1969b, 1970a, 1970b) were directed toward understanding relationships between woody anatomy of herbaceous and woody species of angiosperms with special emphasis on insular forms. Cumbie (1963) reported in detail on cambial activity in *Hibiscus lasiocarpus*; nevertheless, little more has been done to compare continental herbaceous taxa with related woody ones.

The genus *Bigelowia* of the Astereae provides an excellent subject for such a study. These herbaceous rosette plants are frequently monocarpic (particularly so in the greenhouse), and appreciable amounts of secondary xylem are formed only in the caudex. The plants perennate through rhizomaty (in *B. nuttallii*) or produce offsets from the small caudices. (The caudex usually represents one year's growth; two or three growth rings develop only rarely.) Herbaceous forms in the Astereae are probably derived. Carlquist (1960) concluded his survey of the wood anatomy of the tribe with: "the evidence in Astereae, far from countering the well-established woody-to-herbaceous trend in dicots, seems to support it." Data on chromosome numbers reinforce that view (Raven, *et al.*, 1960; Solbrig, *et al.*, 1964, 1969). Near relatives of *Bigelowia* appear to be *Euthamia* and other woodier taxa in the *Haplopappus* alliance (Anderson, 1970); therefore, I used these plants to examine evolutionary trends in a phylad containing woody and herbaceous taxa.

MATERIALS AND METHODS

Living caudices and flowering stems of all taxa in the genus were collected in the field by me or supplied by R. K. Godfrey, S. B. Jones, O. Lakela, or

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TABLE 1. Comparative xylary features from caudices of Bigelowia

Taxon and collection data	age of caudex, yrs.	caudex diameter, mm.	xylem radius, mm.	Vessel elements						Fibers		
				widest diameter, μ	average diameter, μ	average length, μ	average wall thickness, μ	range of pit diameters, μ	average number per group	average diameter, μ	average length, μ	average wall thickness, μ
B. NUTTALLII												
Anderson 3173, Brazos Co., Texas	1	3.02	0.88	24.6	18.0	48.3	3.2	3–5	2.9	13.3	221.4	4.4
Anderson 3089, Turner Co., Ga.	1	3.52	0.76	29.1	17.6	64.4	3.1	4–5	5.2	14.7	199.1	4.5
Godfrey 63191, Washington Co., Fla.	1	3.78	0.88	29.1	20.5	76.1	2.9	4–6	4.3	13.5	180.0	4.5
Thieret 25200, Vernon Par., La.	2	5.80	2.02	44.8	26.1	84.2	3.5	4–5	3.8	11.2	192.6	3.3
Thieret 25186, Natchitoches Par., La.	2	6.04	2.14	42.6	26.9	124.3	3.1	3–5	4.1	12.6	172.7	3.9
Anderson 3464, Pinellas Co., Fla.	2	8.00	2.75	67.2	31.4	141.3	4.2	4–5	4.1	17.8	362.1	5.1

B. NUDATA ssp. NUDATA												
Jones 11071, Forrest Co., Miss.	1	4.28	1.01	33.6	23.4	77.0	2.6	5–7	2.7	14.4	274.4	3.8
Anderson 3088, Turner Co., Ga.	1	6.04	1.26	38.1	26.8	72.3	2.6	5–7	2.0	24.3	238.9	4.1
Anderson 3070, Wakulla Co., Fla.	1	4.78	1.13	38.1	23.5	86.3	2.1	5–10	2.4	19.6	193.6	3.7
Anderson 3263, Onslow Co., N.C.	2	6.12	2.12	44.8	27.6	118.7	2.3	5–8	2.3	15.1	286.7	3.5
B. NUDATA ssp. AUSTRALIS												
Anderson 3471, Pinellas Co., Fla.	1	5.00	0.84	33.6	25.4	65.7	2.1	4–7	1.8	19.9	221.4	3.1
Lakela 30620 Collier Co., Fla.	1	7.30	1.26	47.0	28.9	79.2	2.0	4–7	2.1	20.3	271.4	2.5

J. W. Thieret, whose help is gratefully acknowledged. The larger caudices from each population sample were selected to insure greater xylem development. Material also was taken from the base of the flowering stem and just below the inflorescence for qualitative and quantitative comparisons with the caudex.

Tissues were preserved in FPA, softened in HF, and processed further to prepare slides for examination as in earlier studies (Anderson, 1963; Anderson & Reveal, 1966). Tabular data on cell sizes were obtained by averaging 50 measurements; vessel pit diameters were based on fewer measurements. Each entry in the tables represents a single plant, although more than one was processed for certain collections. Voucher specimens are deposited in the Kansas State University Herbarium (KSC). Additional information on morphology for most collections used in this study is found in Anderson (1970).

RESULTS

Xylem production in *Bigelowia* is not extensive; radial development apparently does not exceed 3 mm. Description of the woods (TABLE 1, FIGURES 1–12, and in the text) is based on study of the caudex. TABLE 2 compares tracheary elements from different regions of the plant body.

Vessels. Average diameter and length of vessel elements in *Bigelowia* are relatively smaller than in most Astereae (Anderson, 1963; Anderson & Reveal, 1966; Carlquist, 1960). The presence of vascular tracheids (practically indistinguishable from narrow vessel elements in transection) can aggravate determination of the average diameter; fortunately they are not common in *Bigelowia*. Most vessels are round in transection; angular ones (fairly typical for Astereae) are infrequent, particularly in *B. nudata*. The relation of wall thickness to diameter in vessels ranges from 11.5 to 17.7% in *B. nuttallii*; 8.3 to 11.1% in *B. nudata* ssp. *nudata*; and 6.9 to 8.3% in *B. nudata* ssp. *australis* (cf. TABLE 1).

The vessel elements all have simple perforation plates. Their end walls generally are transverse to somewhat oblique in orientation; a few of the narrower ones are caudate. Intervascular pits are alternate and have circular to elliptic borders (FIGURE 10); those of *B. nudata* ssp. *nudata* are particularly large for Astereae. Helical sculpture in vessel walls is absent or restricted to fine grooves in *Bigelowia*.

Amount of vessel grouping is varied in Astereae. *Bigelowia* vessels occur singly or in single radial chains (TABLE 1; FIGURES 1–5) as in *Euthamia leptocephala* (Anderson, 1963, as *Solidago leptocephala*). However, in *Chrysothamnus*, a group once thought to be part of *Bigelowia*, vessels are in large, tangentially spread clusters (often more than a dozen per cluster).

Libriform fibers. Dimensions of fibers in *Bigelowia* are most consistent with the average size for the tribe. The relation of wall thickness to fiber width is from 28.7 to 33.3% in *B. nuttallii*; 16.9 to 26.4% in *B. nudata* ssp. *nudata*; and 12.3 to 15.6% in *B. nudata* ssp. *australis*. In *Bigelowia*, fibers

are nonseptate; most retain active protoplasts, resulting in darker staining (FIGURES 7–9). Carlquist (1969a) reported nucleated, septate fibers in the lobelioids. Presence of living fibers, considered an evolutionary advance, may be associated with a reduced amount of axial parenchyma in the xylem (Esau, 1965) or may be an expression of xeromorphy (Fahn, 1964).

Fiber dimorphism with some fibers gelatinous occurs in some *Bigelowia* populations (more frequently in *B. nudata*). Gelatinous fibers can be determined from the amount of shrinkage in the secondary wall, differential staining, and lack of birefringence under polarized light. The gelatinous fibers are similar to the more typical wood fibers in all other ways (i.e., dimensions, original wall thickness, and living state).

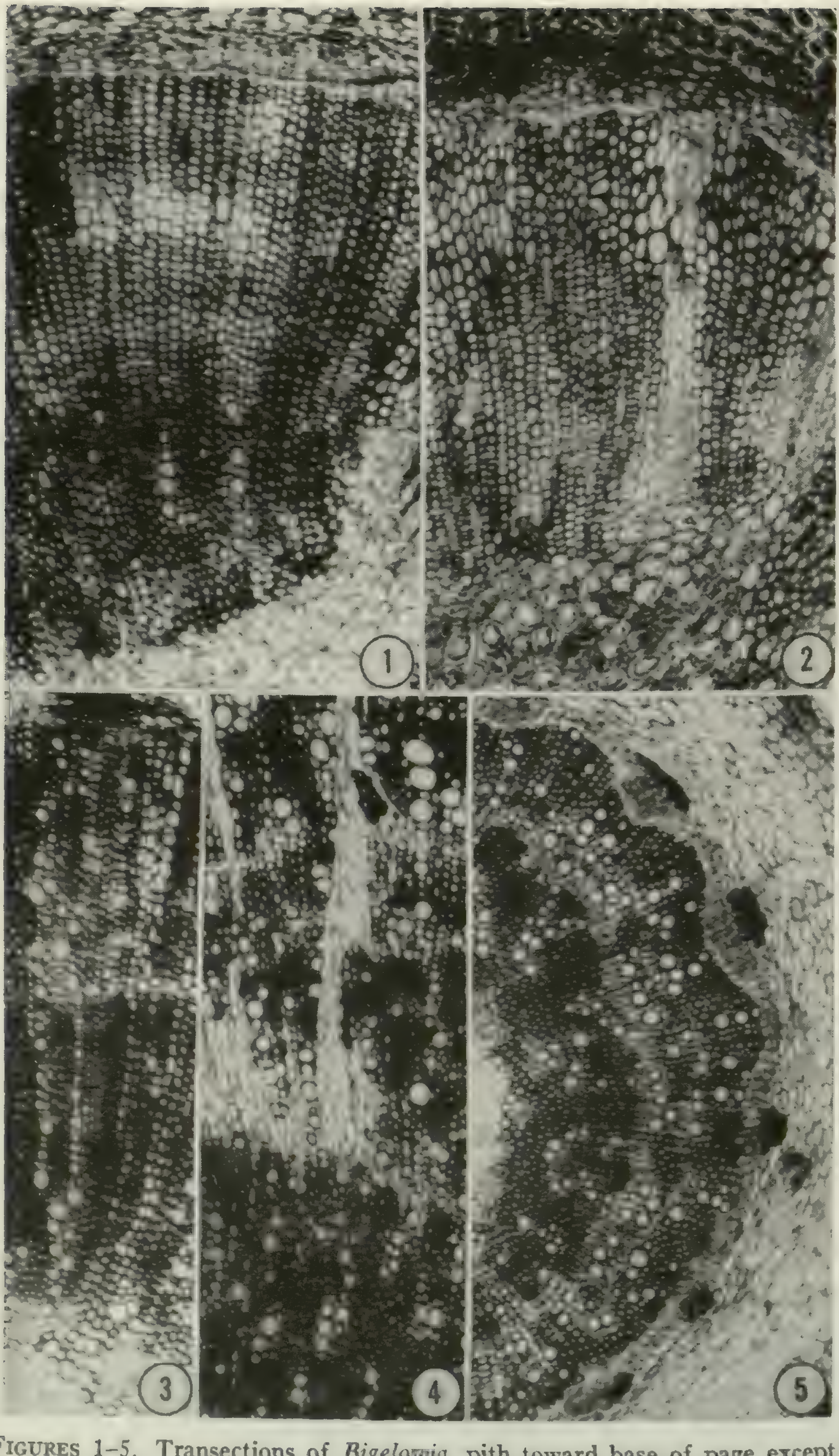
Axial parenchyma. Paratracheal parenchyma is scanty and abaxially vasicentric, which is typical for Astereae and the family (Carlquist, 1960, 1966). Apotracheal parenchyma is present (weakly) as initial bands only in the *B. nuttallii* samples with growth rings (FIGURE 4).

Growth rings. Few caudices live more than a year, those that do, possess growth rings which are not strongly defined. Three years' growth in one caudex of my collection, *Anderson 3464*, is the greatest extent of wood found in the genus; other plants of that population had two years' growth (cf. TABLE 1). The wood is diffuse porous (FIGURES 3–5), and vessel diameter shows only slight fluctuation associated with annual ring formation. Fibers produced at the close of the first growing season, however, are noticeably smaller than those produced at the beginning of the second season. Quantitative and qualitative changes in the rays also accentuate the demarcation line (FIGURES 4, 12).

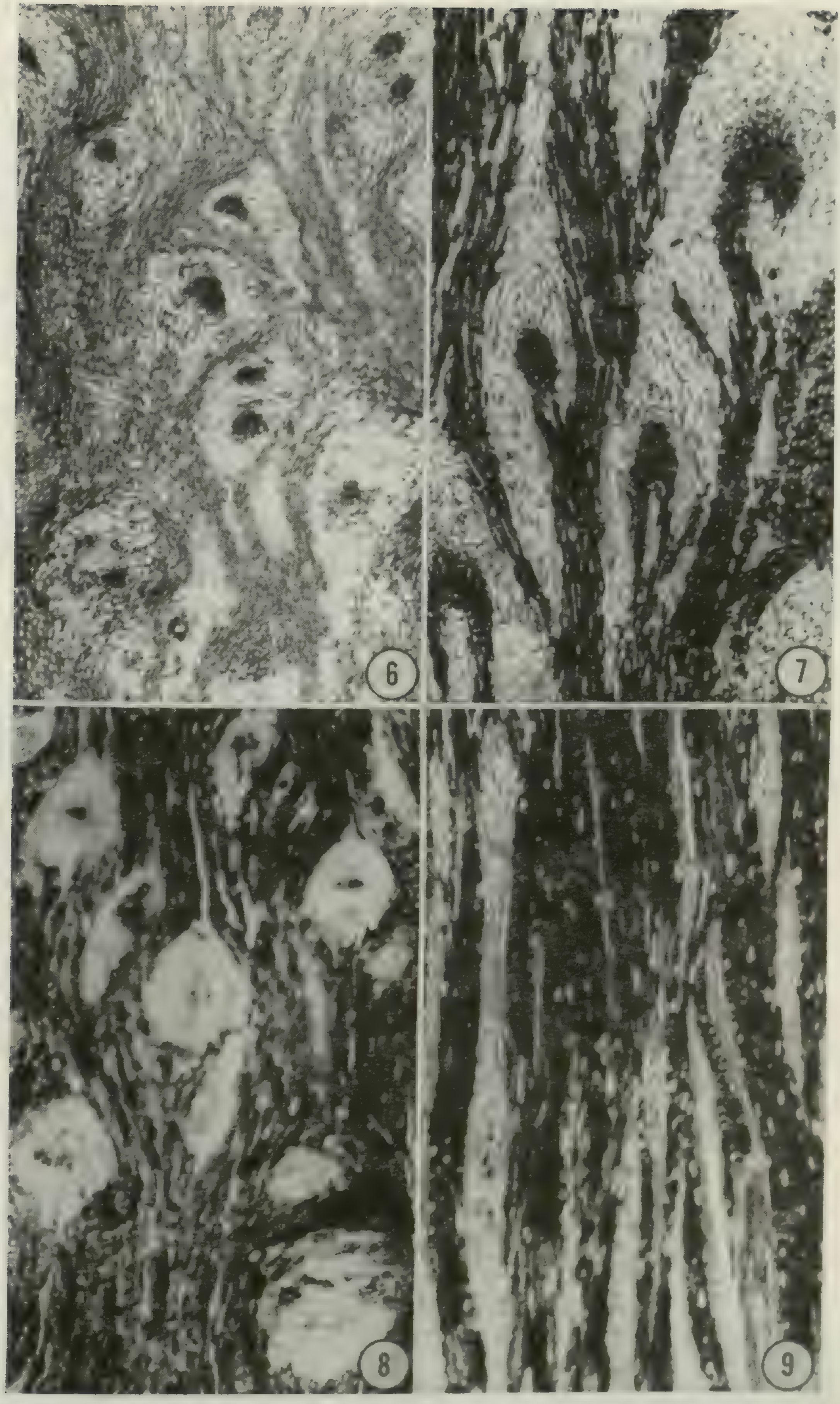
Wood rays. The very nature of the radial system seems to depend on a predisposition of the caudex to be annual or perennial. Differences between rays of one-year-old and two-year-old samples are striking. Such dichotomy also is evident in the general xylary growth pattern in the caudex (see below).

Rays of one-year-old caudices of all taxa always contain vascular traces to adventitious roots and basal leaves (FIGURES 6–8, 11). These rays possibly are merely extensions of gaps in the primary vascular system. Parenchyma surrounding the traces in the ray is loosely oriented, similar to the ground tissue of the pith, and mostly cuboidal to vertically elongated when seen in radial view. Transfusion cells (FIGURE 11) similar to those in *Brighamia* (Carlquist, 1962) are present. The vascular traces and associated parenchyma hardly seem products of the cambium. In a sense then, the wood could be termed rayless. Wood in rhizomes of *Bigelowia nuttallii* (the only species having them), including the single two-year-old rhizome found in *Anderson 3173* (FIGURE 5), is rayless. Rayless rhizomes have been reported for *Euthamia leptocephala* (Anderson, 1963).

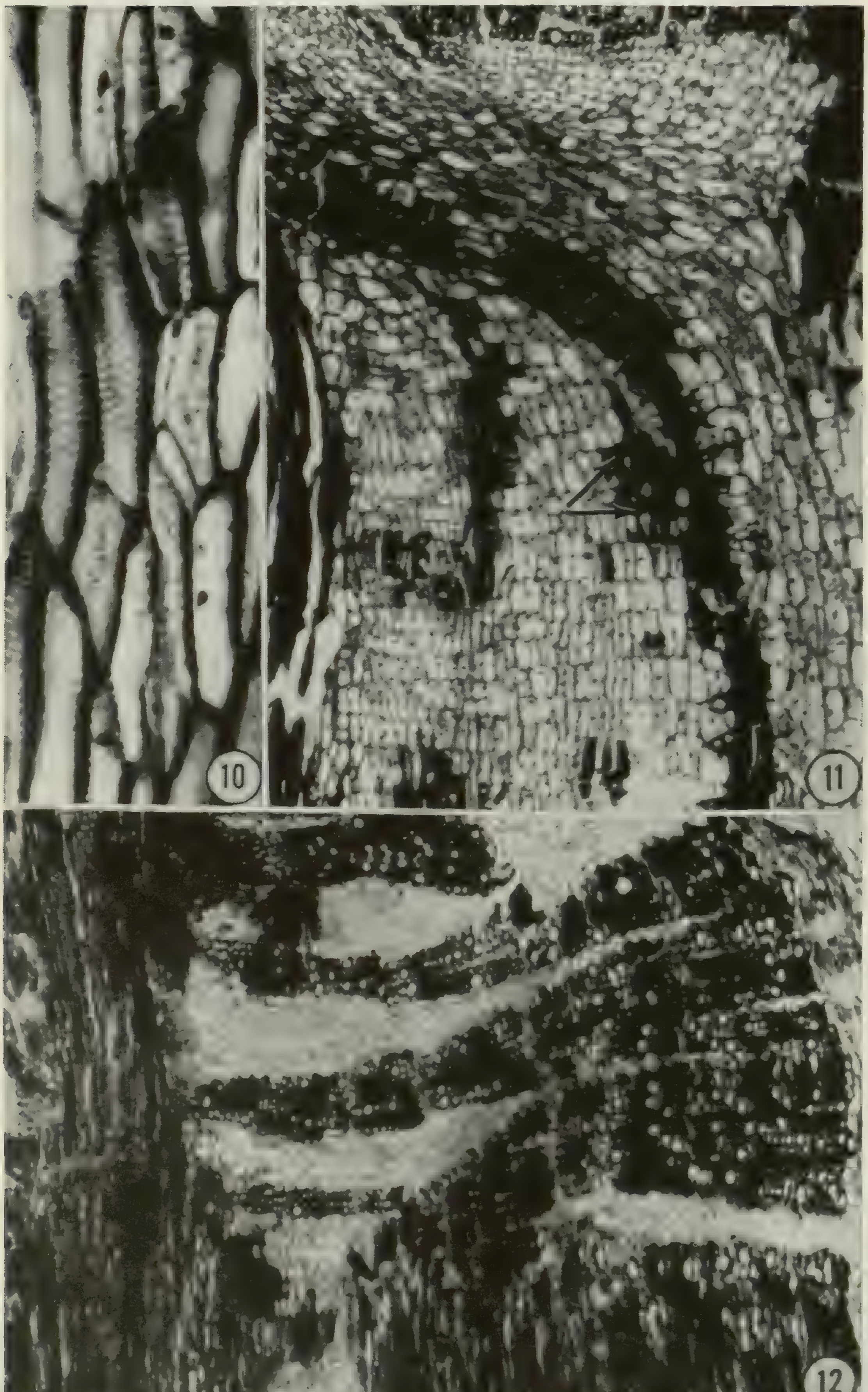
Woods from perennial caudices have relatively greater ray development. However, very few of the rays have included vascular traces; most have none. The rays are multiseriate, averaging four to six cells in width



FIGURES 1–5. Transections of *Bigelowia*, pith toward base of page except in FIGURE 5. 1, *B. nudata* ssp. *nudata* (*Anderson 3070*); 2, *B. nudata* ssp. *australis*, caudex (*Lakela 30620*); 3, *B. nudata* ssp. *nudata*, two-year caudex (*Anderson 3263*); 4, *B. nuttallii*, two-year caudex (*Anderson 3464*), note absence of rays in first year's xylem; 5, *B. nuttallii*, two-year rhizome (*Anderson 3173*). All, × 83.



FIGURES 6–9. Tangential sections of caudex. 6, *Bigelowia nudata* ssp. *nudata*, one-year-old sample (*Anderson 3070*) with vertical orientation of tracheary elements greatly distorted by large "rays"; 7, same from material of *B. nudata* ssp. *australis* (*Lakela 30620*); 8, same from material of *B. nuttallii* (*Godfrey 63191*); 9, two-year-old sample of *B. nuttallii* (*Anderson 3464*) with tall wood rays. All, × 32.



FIGURES 10–12. 10, *Bigelowia nudata* ssp. *australis*, vessel elements with large pits (*Lakela 30620*), × 200; 11, radial section of one-year-old caudex of *B. nuttallii* (*Anderson 3089*) with pith toward left side of page showing "ray" consisting of vertically oriented parenchyma, transfusion cells (arrows), and

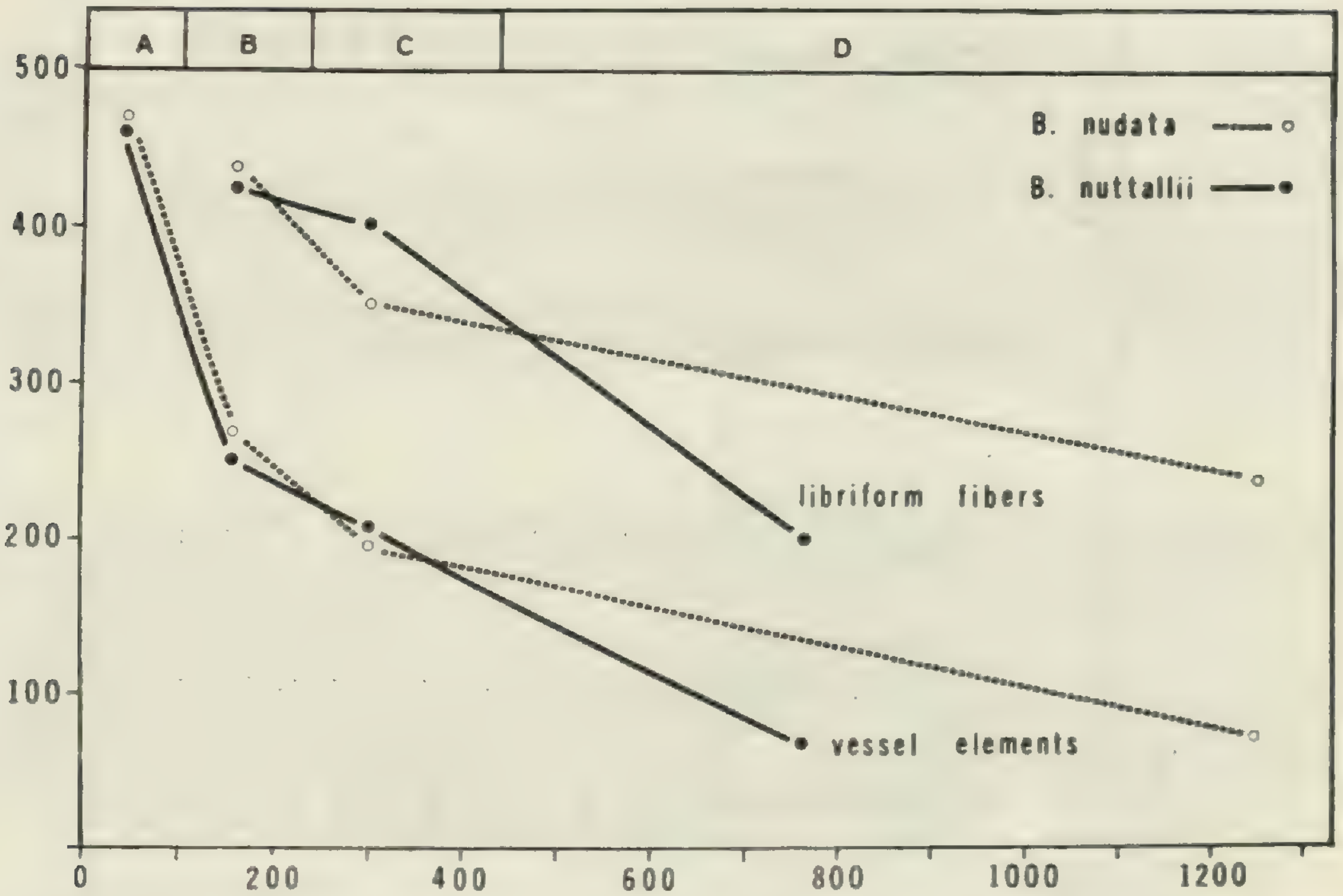


FIGURE 13. Comparison of average tracheary element lengths from different zones of the same plant. Ordinate, cell length in microns; abscissa, radial distance from center of stem or caudex in microns. Zone A, metaxylem of upper stem (fibers absent); B, secondary xylem of upper stem; C, secondary xylem of lower region of aërial stem; D, secondary xylem of caudex. Plants studied, *Anderson 3088* (*Bigelowia nudata*) and *Anderson 3089* (*B. nuttallii*), were growing within a few meters of one another. *B. nuttallii* was on shallow, dry soil of sandstone outcrops; whereas *B. nudata* was in a depression filled with peat moss at the margin of the outcrop.

(FIGURES 4, 9), and ranging from 0.6 to 1.5 mm. tall (the taller ones being in *B. nuttallii*). Ray parenchyma is predominantly procumbent (FIGURE 12) rather than being vertically oriented as are most ray cells of one-year-old caudices (FIGURE 11). New rays, initiated at the beginning of each successive year of growth (FIGURES 2, 14), are wider in the spring wood than in summer wood. The propensity for raylessness in *Bigelowia* woods is also suggested by the increased production of rays after the initial year's growth in the perennial caudices. The ontogenetic relationships between early rayless wood and later wood, in which rays had developed, was noted by Barghoorn (1941).

GROWTH PATTERNS

Study of growth forms should involve measurement of variability in tracheary elements among different organs of the plant and also determi-

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vascular trace, × 80; 12, radial section of three-year-old caudex of *B. nuttallii* (*Anderson 3464*) showing absence of wood rays in initial year's xylem (left) and their increased abundance in each subsequent growth ring, rays composed of predominantly procumbent cells, × 40.

TABLE 2. Xylem data from different tissues in Bigelowia

Taxon				Vessel elements						Fibers		
collection	sample	sample diameter, mm.	xylem radius, mm.	widest diameter, μ	average diameter, μ	average wall thickness, μ	average length, μ	range of pit diameters μ	average number per group	average diameter, μ	average wall thickness, μ	average length, μ
B. NUTTALLII												
Anderson 3173	high stem	1.38	0.20	30.2	22.1	2.4	185.3	3–4	2.3	12.3	3.7	349.4
	low stem	2.22	0.40	31.4	23.5	3.1	146.5	3–4	3.2	13.0	3.7	243.7
	caudex	3.02	0.88	24.6	18.0	3.2	48.3	3–5	2.9	13.3	4.4	221.4
	rhizome	1.93	0.52	38.1	27.1	3.1	94.8	3–4	2.0	11.4	3.4	347.2
Anderson 3089	high stem	1.50	0.14	40.3	30.6	3.4	246.4	4–5	3.3	14.4	4.4	423.3
	low stem	2.00	0.19	38.1	23.4	3.4	204.6	4–5	4.9	14.3	4.6	401.0
	caudex	3.52	0.76	29.1	17.6	3.1	64.4	4–5	5.2	14.7	4.5	199.1
Godfrey 63191	high stem	1.80	0.32	44.8	30.2	3.0	177.5	4–5	3.4	12.3	4.6	342.1
	low stem	1.92	0.38	29.1	21.3	2.9	131.8	4–5	5.3	13.5	4.4	291.2
	caudex	3.78	0.88	29.1	20.5	2.9	76.1	4–6	4.3	13.5	4.5	180.0

B. NUDATA ssp. NUDATA												
Anderson 3088	high stem	1.68	0.14	44.8	30.5	2.2	267.7	3–6	2.3	23.3	6.1	434.3
	low stem	2.50	0.24	47.0	31.9	2.3	198.0	4–6	2.7	19.0	4.4	353.4
	caudex	6.04	1.26	38.1	26.8	2.6	72.3	5–7	2.0	24.3	4.1	238.9
Anderson 3070	high stem	0.85	0.11	35.8	26.4	2.1	314.8	5–6	2.2	15.8	3.2	417.0
	low stem	1.90	0.30	44.2	31.4	2.5	190.4	4–8	2.3	18.9	6.1	256.9
	caudex	4.78	1.13	38.1	23.5	2.1	86.3	5–10	2.4	19.6	3.7	193.6
B. NUDATA ssp. AUSTRALIS												
Lakela 30620	high stem	2.52	0.19	44.8	35.0	2.4	313.6	5–9	1.8	16.3	3.6	436.7
	low stem	3.58	0.60	35.9	26.1	2.6	189.3	5–10	1.9	18.5	2.4	297.7
	caudex	7.30	1.26	47.0	28.9	2.0	79.2	4–7	2.1	20.3	2.5	271.4

nation of patterns of change in element length during growth in a given organ. Variability among different organs or plant regions is tabulated in TABLE 2. Growth patterns, as depicted by average tracheary element lengths in different plant zones, are shown for *Bigelowia nuttallii* and *B. nudata* in FIGURE 13; patterns of change during growth in element length in the caudex are shown in FIGURE 14.

Considerable dissimilarity might be expected in tracheary elements from different regions of the plant when their ontogeny and environment are examined. The aërial (flowering) stem grows rapidly in a single season and is in a more xeric environment than the caudex or rhizome. The high stem (cf. TABLE 2), just below the branches of the inflorescence, has limited cambial activity; the secondary xylem (zone B of FIGURE 13), less abundant than the primary xylem, contains vessel elements and fibers, fibers being absent in the primary xylem (zone A, FIGURE 13). The low stem zone, arbitrarily taken 2 cm. above the caudex has little secondary xylem (zone C, FIGURE 13), but more than does the high stem. The caudex grows more slowly and accumulates the greatest amount of xylem in the plant (zone D, FIGURE 13). The rhizome of *Anderson 3173* (FIGURE 5) has wider vessels but narrower fibers than do other plant regions. In all taxa, vessel members from the aërial stems are generally wider and longer than those of the caudices, whereas fibers are narrower but longer. Vessel wall thickness is rather uniform throughout different zones of the same plant, although the vessels of the caudices, being narrower, have relatively thicker walls.

The assumption that the caudex is more or less predestined to be either annual or perennial is reinforced in the growth patterns of the secondary xylem of both species (FIGURE 14). The fusiform cambial initials of the annual samples and, consequently, the vessel elements they produce become progressively shorter during the growing season. Note that shortening is not so pronounced in the caudices of *Anderson 3088* and *Anderson 3089* (FIGURE 14) as in the different zones of the same plants (FIGURE 13). Cambial initials and vessel elements of the two-year-old caudices in FIGURE 14, on the contrary, become successively longer during the first growing season, and the trend is continued in the second season. In all samples studied, the terminal growth of the two-year-old caudices contained longer vessel elements than did the one-year-old caudices (TABLE 1). Libriform fibers do not necessarily indicate the size of the cambial initials that produce them because fibers exhibit varying amounts of intrusive growth during differentiation and maturation.

DISCUSSION

Trends in xylem evolution in Asteraceae seem rather closely controlled by environmental factors and paedomorphosis, i.e., shifts in wood anatomy related to change in lengths of cambial initials (Carlquist, 1966). Discussion of these factors is an appropriate prelude to taxonomic considerations.

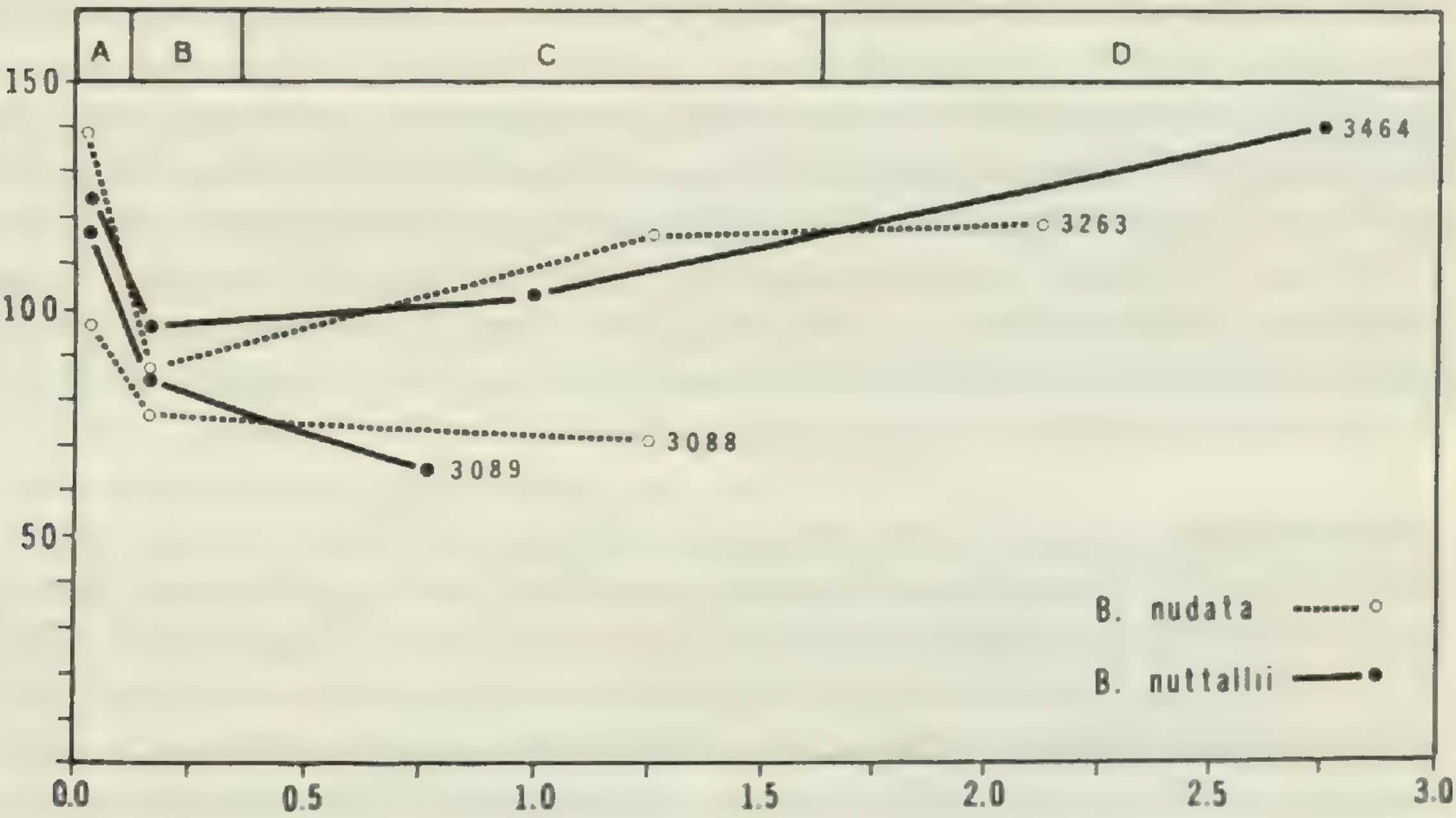

FIGURE 14. Average vessel element length from different positions within the caudex. Ordinate, element length in microns; abscissa, distance from caudex center in millimeters. Zone A, metaxylem; B, first-formed secondary xylem; C, last-formed secondary xylem of first year's growth (total growth for some); D, last-formed xylem of second year's growth. Note shift in growth pattern between annual and perennial caudices during first year's growth.

Ecological anatomy. Fragmentary observations on the ecology of *Bigelowia* (Harper, 1911; Anderson, 1970) indicate that the general environments of the taxa are similar. The range of *B. nuttallii* extends farther west (into Texas) than the range of *B. nudata*. (That western zone is somewhat warmer and drier, as suggested from mean annual temperature and rainfall data.) The species are closely sympatric at one locality in Florida (Harper, 1911) and at scattered stations in southern Georgia, where they differ in habital preferences. The soils on rock outcrops where *B. nuttallii* grows are usually reddish-brown sandy loams with little organic matter (0.5–2.5%) and low cation exchange capacity. Soils where *B. nudata* grows are usually gray sandy loams with more organic matter (2.0–5.0%) and greater cation exchange capacity.

The sunny, open sites where *Bigelowia nuttallii* grows on shallow, better-drained soils are definitely more xeric than those where *B. nudata* grows. Considerable xeromorphy is shown in root and leaf anatomy (Anderson, unpublished) of *B. nuttallii* and is reflected in these anatomical features of the wood: 1) narrow, frequently short vessel elements with thick walls and narrow pits; 2) a number of vessels per group; 3) a number of vascular tracheids; and 4) narrow, short fibers with thick walls. The greater amount of living fibers might also reflect xeromorphism when compared to that of *B. nudata*, but the taller wood rays in the perennial caudices certainly do not. Helical sculpture on vessel walls tends to be more abundant or elaborate in xerophytic composites (Carlquist, 1966), but no taxa of *Bigelowia* have much helical sculpture.

Differences in wood anatomy among different zones of an individual plant may relate to xeromorphy or to patterns of growth involving paedomorphosis. For example, longer tracheary elements in the rhizomes than in the caudex of *Bigelowia nuttallii* (TABLE 2) probably reflect more mesic conditions in the underground as opposed to above-ground habitats. The production of longer vessel elements in higher zones of the aërial stem (FIGURE 13) could relate to juvenilistic growth patterns (paedomorphosis) rather than to influences of the external environment. Carlquist (1970a) suggested this was the case in *Echium pininana*.

Woodiness vs. paedomorphosis. Carlquist (1962), in promulgating his theory of paedomorphosis, pointed out that rosette trees and woody herbs commonly have different growth patterns than do woody plants. The shift in the growth pattern through loss of the marked reduction in cambial fusiform-initial length at the onset of secondary growth results in secondary woods with longer vessel elements than found in related, truly woody plants (FIGURE 15, adapted from Carlquist, 1966).

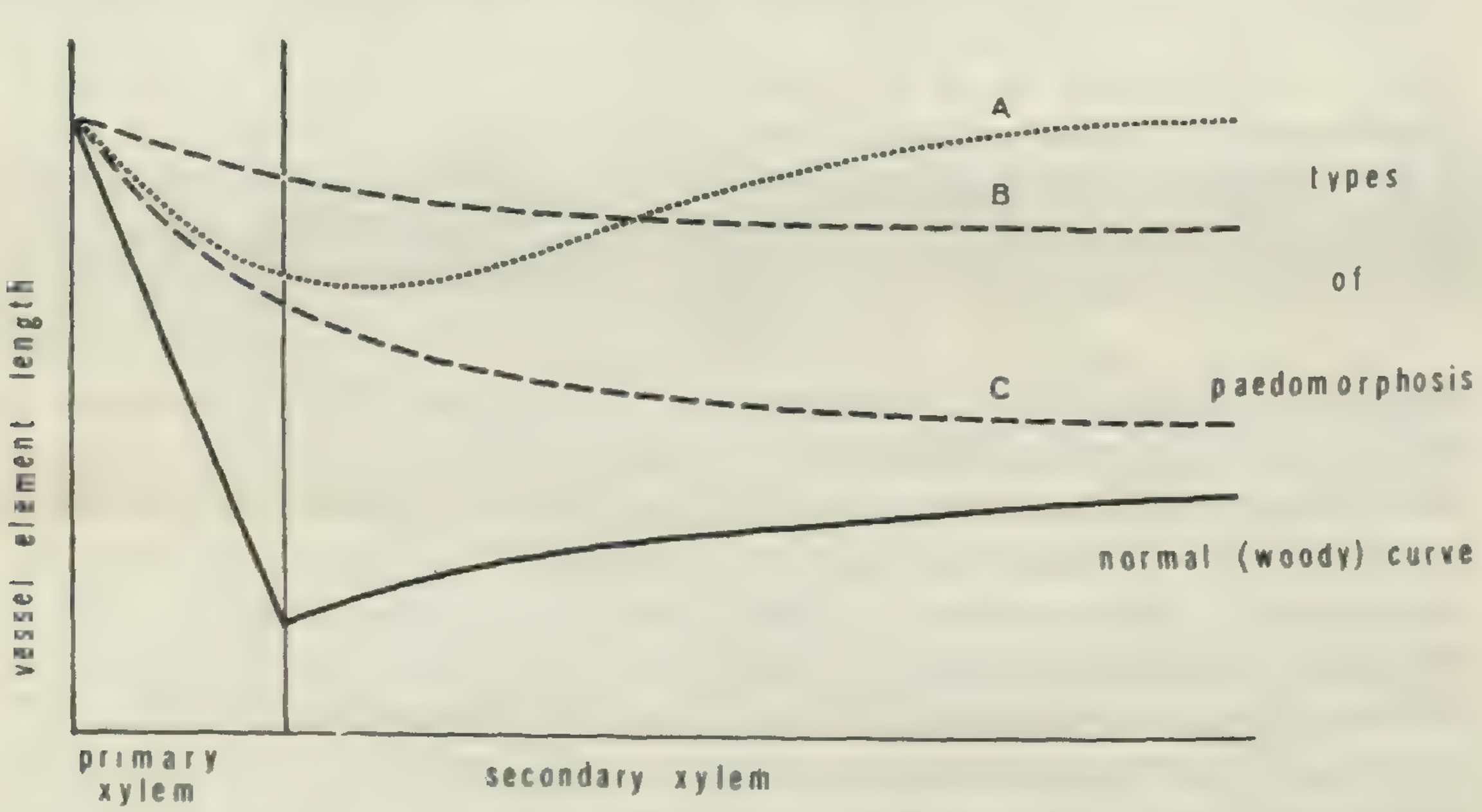

FIGURE 15. Patterns of change in average vessel element length during growth of plant (adapted from Carlquist, 1966).

Such patterns are discomforting to phylogenists. Woody plants, being *generally* more primitive, *generally* have longer cambial initials and, thereby, longer vessel elements than do related, less woody plants. Yet through paedomorphosis, a derived herbaceous plant might have longer vessel elements than related more woody taxa.

Carlquist (1962) suggested that woods influenced by paedomorphosis cannot be compared with those from woody plants because "phylesis both toward and away from herbaceousness would involve juvenile expressions, so these could not be used as criteria of one ancestry or the other." *If* this proves universally true, then woods of woody and herbaceous members of a genus cannot be compared. However, these studies in *Bigelowia*

show that both juvenilistic and woody patterns are found in different plants of the same species (FIGURE 14).

Annual caudices in *Bigelowia* show influence of paedomorphosis through their flattened growth curve (somewhat similar to pattern C of FIGURE 15); the resulting shorter vessel elements, compared with those of the perennials, represent a deviation from the patterns of paedomorphosis as Carlquist described them. These additional characters of the annual caudices also indicate paedomorphosis: pits with wide apertures on vessel elements, presence of transfusion cells, tendency toward raylessness with rays containing vascular traces, and erect ray cells.

The normal (woody) pattern of change in vessel element length is found in the perennial caudices. In addition, woodiness as opposed to paedomorphosis is indicated by longer vessel elements, absence of transfusion cells, and "typical" wood rays with predominantly procumbent ray cells.

In the case of *Bigelowia*, a trend from woodiness to herbaceousness and paedomorphosis is apparent and is related to the shortening of the life of the caudex.

Phylogenetic considerations. *Bigelowia nuttallii* and *B. nudata* are closely related; artificial, sterile hybrids between the species have been produced (Anderson, unpublished). If one species were to be considered more primitive, based on data from wood anatomy, it would be *B. nuttallii* which has generally longer vessel elements (even though probably shortened through xeromorphism); also, a greater number of perennials have been found in that species.

Woodiness may appropriately be designated a primitive feature for *Bigelowia*, as apparently it is for the tribe (Carlquist, 1960). *Euthamia* has been suggested as a close relative of *Bigelowia* (Anderson, 1970). Patterns of change in vessel element length during growth have been determined for plants of *E. graminifolia* and *E. leptocephala* (Anderson, unpublished); interestingly, both have a normal (woody) growth curve.

More than a quarter of a century ago, Tippo (1946), in discussing the role of wood anatomy in phylogeny, stated:

> The next logical development which may be expected in this field of endeavor is a series of exploratory investigations of the herbaceous Dicotyledons whose purpose will be not only to uncover new phylogenetic sequences, but to extend the lines of specialization already established into the relatively virgin territory. There is every reason to suppose that the trends already defined will be found to prevail in the secondary wood of the herbs, and there is also some basis for belief that similar sequences will be unearthed in the primary xylem.

Knowledge of wood anatomy in herbaceous plants is still so limited that we do not know how universal paedomorphosis is or what other patterns may be found. Certainly they will not parallel the trends already established for woody dicots, as Tippo supposed they would.

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NOTES ON WEST INDIAN ORCHIDS, III *

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IN PREPARING THE generic descriptions of orchids for the projected *Flora of the Lesser Antilles* by Dr. Richard A. Howard of Harvard University, it became necessary to typify each generic name reported from that area in order to arrive at a correct circumscription. During our studies we have found that some of the early lectotypifications are incorrect due to random choices. Indirect lectotypifications through the removal of specific epithets by transfers have also been ignored. We have compared and have brought each known typification into line with the principles expressed in the "Guide for the determination of types," published in the *International Code of Botanical Nomenclature*. As a result of this procedure we are presenting with sundry comments a list of typifications of those generic names of orchids (whether currently accepted or synonymous) which are reported from the West Indies, the Greater Antilles and the Lesser Antilles, excluding Trinidad, Tobago, and the off-shore continental islands of northern South America.

Achroanthes Raf. in Am. Monthly Mag. Crit. Rev. **4**: 195. Jan. 1819.
TYPE: *Malaxis ophioglossoides* Willd.
OBSERVATION: This name is based on *Malaxis* subgenus *Microstylis* Nutt. The name was rejected in 1954 in favor of *Microstylis* (Nutt.) A. Eaton. It is a synonym of **Malaxis** Soland. ex Sw.

Acraea Lindl. in Benth. Pl. Hartweg. 155. Aug. 1845.
TYPE: *Acraea parvifolia* Lindl.
OBSERVATION: It is a synonym of **Pterichis** Lindl.

Adnula Raf. Fl. Tellur. 2: 87. Jan.–Mar. 1837.
TYPE: *Satyrium adnatum* Sw.
OBSERVATION: A superfluous name based on the type of the genus *Pelexia* Poit. ex Lindl. It is a synonym of **Spiranthes** L. C. Rich.

Alipsa Hoffmsgg. Verz. Orch. 20. 1842.
TYPE: *Ophrys Loeselii* L.
OBSERVATION: This is an illegitimate name and a synonym of **Liparis** L. C. Rich.

Amalia Rchb. Herbarienb. Nomencl. 52. no. 1974. July 1841.
LECTOTYPE: *Bletia grandiflora* La Llave & Lex.
OBSERVATION: This is a new name for *Laelia* Lindl. 1831, not Adanson 1763. The name was rejected in 1935; it is a synonym of **Laelia** Lindl.

* In this series, No. I was published in the Journal of the Arnold Arboretum **50**: 462–468. 1969; No. II, *Ibid.* **53**: 390–398. 1972.

Amphiglottium Lindl. ex Stein, Orchideenbuch 66. 1892.
TYPE: *Epidendrum secundum* Jacq.
OBSERVATION: It is a synonym of **Epidendrum** L.

Anacheilium Hoffmsgg. Verz. Orch. 21. 1842.
TYPE: *Epidendrum cochleatum* L.
OBSERVATION. It is a synonym of **Epidendrum** L.

Arpophyllum La Llave & Lex. Nov. Veg. Descr. Orch. Opus 2: 19. 1825.
TYPE: *Arpophyllum spicatum* La Llave & Lex.

Auliza Salisb. ex Small, Fl. Miami 55. Apr. 26, 1913.
TYPE: *Epidendrum nocturnum* L.
OBSERVATION: It is a synonym of **Epidendrum** L.

Aulizeum Lindl. ex Stein, Orchideenbuch 84. 1892.
TYPE: *Epidendrum ciliare* L.
OBSERVATION: It is a synonym of **Epidendrum** L.

Basiphyllaea Schltr. in Fedde Repert. Sp. Nov. 17: 77. Apr. 1, 1921.
TYPE: *Bletia sarcophylla* Rchb. f.

Beadlea Small, Fl. SE. U.S. 319. July 1903.
TYPE: *Spiranthes Storeri* Chapm.
OBSERVATION: It is a synonym of **Spiranthes** L. C. Rich.

Bletia Ruíz & Pav. Fl. Peru. Prodr. 119. *t.26*. Oct. 1794.
LECTOTYPE: *Bletia catenulata* Ruíz & Pav.
OBSERVATION: Lectotype was chosen by Britton & Millspaugh, Bahama Flora 96. 1920.

Brachionidium Lindl. Folia Orch. Brachionidium 1. Mar. 10, 1859.
LECTOTYPE: *Restrepia parvifolia* Lindl.
OBSERVATION: Lectotype was chosen by Garay in Canad. Jour. Bot. **34**: 729 1956.

Brassavola R. Br. in Ait. Hort. Kew. ed. 2. **5**: 215. Dec. 1813.
TYPE: *Epidendrum cucullatum* L.

Brassia R. Br. in Ait. Hort. Kew. ed. 2. **5**: 215. Dec. 1813.
TYPE: *Brassia maculata* R. Br.

Broughtonia R. Br. in Ait. Hort. Kew. ed. 2. **5**: 217. Dec. 1813.
TYPE: *Epidendrum sanguineum* Sw.

Bolbophyllaria Rchb. f. in Bot. Zeit. **10**: 934. Dec. 31, 1852.
TYPE: *Bulbophyllum bracteolatum* Lindl.
OBSERVATION: This is a synonym of **Bulbophyllum** Thou.

Bulbophyllum Thou. Hist. Pl. Orch. trois. tabl. esp. Mar. 11, 1822.
LECTOTYPE: *Bulbophyllum nutans* Thou.
OBSERVATION: The genus was conserved in 1905. The lectotype was chosen by Green, Prop. Brit. Bot. 100. 1929.

Burlingtonia Lindl. in Bot. Reg. 23: *t. 1927*. Jan. 1, 1837.
TYPE: *Burlingtonia candida* Lindl.
OBSERVATION: This is a synonym of **Rodriguezia** Ruíz & Pav.

Calanthe R. Br. in Bot. Reg. 7: sub *t. 573*. Oct. 1, 1821.
TYPE: *Orchis triplicata* Willem.
OBSERVATION: The genus was conserved in 1905.

Calopogon R. Br. in Ait. Hort. Kew. ed. 2. **5**: 204. Dec. 1813.
TYPE: *Limodorum tuberosum* L.
OBSERVATION: The genus was conserved in 1905.

Camaridium Lindl. in Bot. Reg. 10: *t. 844*. Nov. 1, 1824.
TYPE: *Camaridium ochroleucum* Lindl.
OBSERVATION: This is a synonym of **Maxillaria** Ruíz & Pav.

Campylocentrum Benth. in Jour. Linn. Soc. Bot. 18: 337. Feb. 23, 1881.
TYPE: *Todaroa micrantha* Rich. & Gal.
OBSERVATION: This is a new name for *Todaroa* Rich. & Gal. 1845, not Parlatore 1843.

Carteria Small in Torreya 10: 187. Aug. 1910, not Diesing 1866.
TYPE: *Carteria corallicola* Small.
OBSERVATION: This is a synonym of **Basiphyllaea** Schltr.

Cattleya Lindl. Coll. Bot. *t. 33*. 1821.
TYPE: *Cattleya labiata* Lindl.

Cattleyopsis Lem. Jard. Fleur. 4: Misc. p. 59, no. 165. Aug. 1, 1853.
TYPE: *Cattleyopsis delicatula* Lem.

Centrogenium Schltr. in Beih. Bot. Centralbl. 37(2): 451. Mar. 31, 1920.
LECTOTYPE: *Neottia calcarata* Sw.
OBSERVATION: Lectotype was chosen by Correa in Darwiniana 11: 81. 1955. This is a synonym of **Eltroplectris** Raf.

Chloidia Lindl. Gen. and Sp. Orch. Pl. 484. Sept. 1840.
LECTOTYPE: *Serapias polystachya* Sw.
OBSERVATION: Lectotype was chosen indirectly by Cogniaux in Martius Fl. Bras. 3(4): 276. 1895. This is a synonym of **Tropidia** Lindl.

Chloraea Lindl. in Quart. Jour. Sci. 23: 47. Mar. 1827.
TYPE: *Cymbidium luteum* Willd.
OBSERVATION: The genus *Chloraea* was first suggested by Lindley in his Collectanea Botanica Appendix No. 12. Jan. 1826. He clearly indicated that he was basing it on "*Epipactis &c Gavilu, Feuillée.*" This reference is applicable only to two plants depicted by Feuillée in Jour. Observ. Bot. 2: 1714; the first on *t. 18* as *Epipactis flore albo vulgo Gavilu*, and the second on *t. 20* as *Epipactis amplo flore luteo, vulgo Gavilu.*

In describing the genus *Chloraea*, Lindley included among the nine species only one of Feuillée's plants, namely the second polynomial mentioned on plate 20, calling it *Chloraea Gavilu* Lindl. Unfortunately this is an illegitimate name for Lindley included *Cymbidium luteum* Willd., also based on the same polynomial, in synonymy.

The recent choice of *Cymbidium virescens* Willd. for a lectotype by Correa in Flora Patagonica 7(2): 200. 1970, is incorrect.

Cleistes L. C. Rich. ex Lindl. Gen. and Sp. Orch. Pl. 409. Feb. 1840.
TYPE: *Limodorum grandiflorum* Aubl.
OBSERVATION: Type was originally suggested by L. C. Richard, Orch. Eur. Annot. 9. 1817.

Cochleanthes Raf. Fl. Tellur. 4: 45. (July) 1838.
TYPE: *Zygopetalum cochleare* Lindl.

Coelia Lindl. Gen. and Sp. Orch. Pl. 36. Apr. 1830.
TYPE: *Epidendrum tripterum* Sm.

Comparettia Poepp. & Endl. Nov. Gen. ac Sp. Pl. 1: 42. May 28, 1836.
LECTOTYPE: *Comparettia falcata* Poepp. & Endl.
OBSERVATION: Lectotype was chosen indirectly by Reichenbach in Walp. Ann. Bot. Syst. 6: 689. 1863, when he transferred *C. saccata* Poepp. & Endl. to the genus *Scelochilus*. Therefore, the lectotypification by Britton & Wilson, Sci. Surv. Porto Rico 5(2): 211. 1924 is not tenable.

Corallorrhiza Gagneb. in Acta Helv. 2: 61. Feb. 1755.
TYPE: *Ophrys Corallorhiza* L.

Corydandra Rchb. Herbarienb. Nomencl. 53. no. 2047. July 1841.
TYPE: *Galeandra Baueri* Lindl.
OBSERVATION: This is merely an illegitimate new name for **Galeandra** Lindl.

Corymborkis Thou. in Nouv. Bull. Sci. Soc. Philom. Paris, ser. 2. 1: 318. Apr. 1809.
TYPE: *Corymborkis corymbosa* Thou.
OBSERVATION: The type is provided in Thou. Hist. Pl. Orch. *t. 37*. 1822.

Cranichis Sw. Nov. Gen. & Sp. Pl., Prodr. 8. July 1788.
LECTOTYPE: *Cranichis muscosa* Sw.
OBSERVATION: Lectotype was chosen by Acuña in Bol. Tec. Cuba 60: 48. 1939.

Cryptarrhena R. Br. in Bot. Reg. 2: *t* .153. Nov. 1, 1816.
TYPE: *Cryptarrhena lunata* R. Br.

Cryptophoranthus Barb. Rodr. Gen. et Sp. Orch. Nov. 2: 79. 1882.
LECTOTYPE: *Pleurothallis fenestrata* Barb. Rodr.
OBSERVATION: Lectotype was chosen by Acuña in Bol. Tec. Cuba 60: 115. 1939.

Cybelion Spreng. Syst. Veg. 3: 679. Jan–June 1826.
TYPE: *Ionopsis pulchella* H. B. K.
OBSERVATION: This is an illegitimate new name for **Ionopsis** H. B. K. and is a synonym of that generic name.

Cyclopogon Presl, Rel. Haenk. 1: 93. 1827.
TYPE: *Cyclopogon ovalifolium* Presl.
OBSERVATION: This is a synonym of **Spiranthes** L. C. Rich.

Cycloptera Endl. ex Jackson in Ind. Kew. 1: 680. Sept. 6, 1893.
TYPE: *Cyclopogon ovalifolium* Presl.
OBSERVATION: This is a synonym of **Spiranthes** L. C. Rich.

Cyrtopera Lindl. Gen. and Sp. Orch. Pl. 189. Jan. 1833.
LECTOTYPE: *Cyrtopodium Woodfordii* Sims.
OBSERVATION: Lectotype was chosen by A. Richard in D'Orbigny, Dict. Hist. Nat. 4: 561. 1844. This is a synonym of **Eulophia** R. Br.

Cyrtopodium R. Br. in Ait. Hort. Kew. ed. 2. 5: 216. Dec. 1813.
TYPE: *Cymbidium Andersonii* Lamb. ex Andr.

Dendrophylax Rchb. f. in Walp. Ann. Bot. Syst. 6: 903. Dec. 1864.
TYPE: *Dendrophylax hymenanthus* Rchb. f.

Dichaea Lindl. Gen. and Sp. Orch. Pl. 208. Apr. 1833.
TYPE: *Epidendrum echinocarpum* Sw.
OBSERVATION: The type was suggested by Lindley first in Bot. Reg. 18: sub *t. 1530.* Oct. 1, 1832. Lindley described *Dichaea* a second time in Hook. Jour. Bot. 1: 5. 1834 with *D. panamensis* as the type.

Dichaeopsis Pfitzer, Entwurf Nat. Anord. Orch. 93. 1887.
LECTOTYPE: *Epidendrum graminoides* Sw. *in hoc loco.*
OBSERVATION: This is a synonym of **Dichaea** Lindl.

Dicrypta Lindl. Gen. and Sp. Orch. Pl. 44. May 1830.
TYPE: *Dicrypta Baueri* Lindl.
OBSERVATION: This is a synonym of **Maxillaria** Ruíz & Pav.

Dienia Lindl. in Bot. Reg. 10: sub *t. 825.* Sept. 1, 1824.
TYPE: *Dienia congesta* Lindl.
OBSERVATION: This is a synonym of **Malaxis** Soland. ex Sw.

Dilomilis Raf. Fl. Tellur. 4: 43. (July) 1838.
TYPE: *Octomeria serratifolia* Hook.

Dinema Lindl. Gen. and Sp. Orch. Pl. 111. Aug. 1831.
TYPE: *Epidendrum polybulbon* Sw.
OBSERVATION: Type originally suggested by Lindley in his Collectanea Botanica, Appendix No. 125. Jan. 1826. The generic name is a synonym of **Epidendrum** L.

Domingoa Schltr. in Urban, Symb. Antill. 7: 496. Aug. 15, 1913.
LECTOTYPE: *Epidendrum hymenodes* Rchb. f.
OBSERVATION: Lectotype was chosen by Acuña in Bol. Tec. Cuba **60**: 64. 1939.

Dothilis Raf. Fl. Tellur. 2: 60 Jan.–Mar. 1837.
TYPE: *Neottia grandiflora* Hook.
OBSERVATION: This is a synonym of **Chloraea** Lindl.

Elleanthus Presl, Rel. Haenk. 1: 97. 1827.
LECTOTYPE: *Elleanthus lancifolius* Presl.
OBSERVATION: Lectotype was chosen by Britton & Wilson, Sci. Surv. Porto Rico 5(2): 203. 1924.

Eltroplectris Raf. Fl. Tellur. 2: 51. Jan.–Mar. 1837.
TYPE: *Neottia calcarata* Sw.

Encyclia Hook. in Bot. Mag. **55**: *t. 2831*. June 1, 1828.
TYPE: *Encyclia viridiflora* Hook.
OBSERVATION: This is a synonym of **Epidendrum** L.

Enothrea Raf. Fl. Tellur. **4**: 43. (July) 1838.
TYPE: *Epidendrum graminifolium* L.
OBSERVATION: This is a synonym of **Octomeria** R. Br.

Epicladium Small, Fl. Miami 56. Apr. 26, 1913.
TYPE: *Epidendrum Boothianum* Lindl.
OBSERVATION: This is a synonym of **Epidendrum** L.

Epidendrum L. Sp. Pl. ed. 1. 2: 952. May 1, 1753 (Aug. 16, 1753).
LECTOTYPE: *Epidendrum nodosum* L.
OBSERVATION: Lectotype was chosen by Britton & Wilson, Sci. Surv. Porto Rico **5**(2): 203. 1924. This generic name was rejected in 1930; it is a synonym of **Brassavola** R. Br.

Epidendrum L. Sp. Pl. ed. 2. 2: 1347. July 1763.
LECTOTYPE: *Epidendrum nocturnum* Jacq.
OBSERVATION: This generic name has been conserved with the above given type in 1930. Lectotype was chosen by Sprague in Prop. Brit. Bot. 53. 1929.

Epistephium Kunth, Syn. Pl. Equinoct. 1: 340. Dec. 9, 1822.
TYPE: *Epistephium elatum* Kunth.

Epithecia Knowles & Westcott, Fl. Cab. 2: 167. Jan. 1839.
TYPE: *Prosthechea glauca* Knowles & Westcott.
OBSERVATION: The type of this genus has been confused with *Epidendrum glaucum* Sw. 1788, because of Lindley's transfer of it to *Epidendrum glaucum* (Knowles & Westcott) Lindl. in 1840. Hence this generic name was considered by Kuntze in 1903 and by Schlechter in 1914 to be a synonym of *Dichaea* Lindl. and *Dichaeopsis* Pfitz. respectively. It is, however, as Lindley's transfer indicates, a synonym of **Epidendrum** L.

Erythrodes Bl. Bijdr. **6**: *t. 1, f. 72*. June 1825.
TYPE: *Erythrodes latifolia* Bl.
OBSERVATION: The type is given by Blume in Bijdr. 8: 411. July 1825.

Eulophia R. Br. ex Lindl. in Bot. Reg. **8**: *t. 686*. Feb. 1, 1823, not Agardh, 1822.
TYPE: *Eulophia guineensis* Lindl.
OBSERVATION: This generic name was conserved in 1905 and typified by Green in 1929 by *Eulophia barbata* Spreng. which was adopted by the 5th International Botanical Congress in 1930. However, *Eulophia barbata* is one of the main species upon which Pfitzer based his new genus *Acrolophia* in 1887. In segregating *Acrolophia*, Pfitzer explicitly typified *Eulophia* by *E. guineensis* Lindl. in his *Entwurf einer natuerlichen Anordnung der Orchideen* p. 59, 1887. Summerhayes and Hall in Taxon **11**: 203. 1962 proposed changing the conserved type from *E. barbata* to *E. guineensis*. No action

has yet been taken by either the 10th or 11th International Botanical Congresses.

Eurystyles Wawra in Oesterr. Bot. Zeitschr. 13: 223. July 1863.
TYPE: *Eurystyles cotyledon* Wawra.

Evelyna Poepp. & Endl. Nov. Gen. ac Sp. Pl. 1: 32. May 28, 1836.
LECTOTYPE: *Evelyna capitata* Poepp. & Endl.
OBSERVATION: Lectotype was chosen by Pfeiffer, Nomencl. Bot. 1(2): 1321. 1874. It is a synonym of **Elleanthus** Presl.

Fractiunguis Schltr. in Anex. Mem. Inst. Butantan, Bot. 1(4): 55. Mar. 1922.
LECTOTYPE: *Hexisea reflexa* Rchb. f.
OBSERVATION: Lectotype was chosen by Acuña in Bol. Tec. Cuba **60**: 89. 1939. This is a synonym of **Reichenbachanthus** Barb. Rodr.

Fuertesiella Schltr. in Urban, Symb. Antill. 7: 492. Aug. 15, 1913.
TYPE: *Fuertesiella pterichoides* Schltr.

Galeandra Lindl. in Bauer & Lindley, Ill. Orch. Pl., Gen. *t. 8*. 1832.
TYPE: *Galeandra Baueri* Lindl.

Ghiesbreghtia Rich. & Gal. in Ann. Sci. Nat. ser. 3. 3: 28. Jan. 1845.
TYPE: *Ghiesbreghtia calanthoides* Rich. & Gal.
OBSERVATION: This is a synonym of **Calanthe** R. Br.

Goodyera R. Br. in Ait. Hort. Kew. ed. 2. 5: 197. Dec. 1813.
LECTOTYPE: *Satyrium repens* L.
OBSERVATION: Lectotype was chosen by Sprague in Jour. Bot. **64**: 113. 1926. This generic name was conserved with the above given lectotype in 1930.

Govenia Lindl. in Lodd. Bot. Cab. **18**: *t. 1709*. July 1831.
TYPE: *Maxillaria superba* La Llave & Lex.

Gyrostachys Pers. ex Bl. Coll. Orch. 127. 1859.
LECTOTYPE: *Ophrys spiralis* L.
OBSERVATION: Lectotype was chosen by O. Kuntze, Rev. Gen. Pl. **2**: 663. 1891. This generic name was rejected in 1905; it is a synonym of **Spiranthes** L. C. Rich.

Habenaria Willd. Sp. Pl. **4**: 44. 1805.
LECTOTYPE: *Orchis Habenaria* L.
OBSERVATION: The correct lectotype was chosen first by Kraenzlin in Engl., Bot. Jahrb. **16**: 58. 1892. The choice of *Orchis monorrhiza* Sw. for the lectotype by Lindley in Bot. Reg. **18**: sub *t. 1499*. 1832, does not carry the appropriate name.

Hapalorchis Schltr. in Beih. Bot. Centralbl. 37(2): 362. Mar. 31, 1920.
LECTOTYPE: *Sauroglossum candidum* Krzl.
OBSERVATION: Lectotype was chosen by Britton & Wilson, Sci. Surv. Porto Rico **5**(2): 186. 1924. Schlechter at the time of publication recognized four species, but all four have been united under *Spiranthes lineata* Lindl. by Garay & Dunsterville, Venez. Orch. Ill. **4**: 278. 1966. This is a synonym of **Spiranthes** L. C. Rich.

Harrisella Fawcett & Rendle in Jour. Bot. 47: 265. July 1909.
TYPE: *Aeranthus porrectus* Rchb. f.
OBSERVATION: This is a synonym of **Campylocentrum** Benth.

Heterotaxis Lindl. in Bot. Reg. 12: *t. 1028*. Dec. 1, 1826.
TYPE: *Heterotaxis crassifolia* Lindl.
OBSERVATION: This is a synonym of **Maxillaria** Ruíz & Pav.

Hexadesmia Brongn. in Ann. Sci. Nat. ser. 2. 17: 44. Jan. 1842.
TYPE: *Hexadesmia fasciculata* Brongn.

Homalopetalum Rolfe in Hook. Icon. Pl. 25: *t. 2461*. May 1896.
TYPE: *Homalopetalum jamaicense* Rolfe.

Hormidium Lindl. ex Haynhold, Nom. Bot. 2: 880. 1840.
TYPE: *Epidendrum uniflorum* Lindl.
OBSERVATION: The type was chosen by Lindley in Bot. Reg. 25: Misc. p. 16. 1839. This is a synonym of **Epidendrum** L.

Humboldtia Ruíz & Pav. Fl. Peru. Prodr. 121. Oct. 1794 ("*Humboltia*"), not Vahl 1794.
LECTOTYPE: *Humboldtia purpurea* Ruíz & Pav., *in hoc loco*.
OBSERVATION: The orthography has been corrected by Ruíz & Pav. Syst. Veg. 233. Dec. 1798. For the explanation of lectotype see **Stelis** Sw. of which it is a synonym.

Ibidium Salisb. ex Small, Fl. SE. U.S. ed. 2. 318. Apr. 23, 1913.
LECTOTYPE: *Ophrys spiralis* L.
OBSERVATION: Lectotype was chosen by House in Bull. Torr. Bot. Club 32: 380. 1905. This is a synonym of **Spiranthes** L. C. Rich.

Ionopsis H. B. K. Nov. Gen. et Sp. Pl. 1: 348. Aug. 1816.
TYPE: *Ionopsis pulchella* H. B. K.

Isochilus R. Br. in Ait. Hort. Kew. ed. 2. 5: 209. Dec. 1813.
LECTOTYPE: *Epidendrum lineare* Jacq.
OBSERVATION: Lectotype was chosen indirectly by Reichenbach in Bonplandia 2: 22. 1854.

Jacquiniella Schltr. in Fedde Repert. Sp. Nov. Beih. 7: 123. Jan. 31, 1920.
LECTOTYPE: *Epidendrum globosum* Jacq.
OBSERVATION: Lectotype was chosen by Britton & Wilson, Sci. Surv. Porto Rico 5(2): 197. 1924.

Koellensteinia Rchb. f. in Bonplandia 2: 17. Jan. 15, 1854.
TYPE: *Koellensteinia Kellneriana* Rchb. f.

Laelia Lindl. Gen. and Sp. Orch. Pl. 115. Aug. 1831, not Adanson 1763.
LECTOTYPE: *Bletia grandiflora* La Llave & Lex.
OBSERVATION: Lectotype was chosen by Dandy in Kew Bull. 86. 1935. This generic name was conserved in 1935.

Laeliopsis Lindl. in Lindl. & Paxton, Fl. Gard. 3: 155. *t. 105*. Jan. 1853.
TYPE: *Cattleya domingensis* Lindl.

Lankesterella Ames, Sched. Orch. **4**: 3. May 4, 1923.
TYPE: *Lankesterella costaricensis* Ames.

Leochilus Knowles & Westcott, Fl. Cab. **2**: 143. Nov. 1838.
TYPE: *Leochilus oncidioides* Knowles & Westcott.

Lepanthes Sw. in Nov. Act. Soc. Sci. Upsala **6**: 85. 1799.
LECTOTYPE: *Epidendrum ovale* Sw. (*Lepanthes concinna* Sw. *nom. illeg.*)
OBSERVATION: Lectotype was chosen by Britton & Wilson, Sci. Surv. Porto Rico **5**(2): 206. 1924.

Lepanthopsis Ames in Bot. Mus. Leafl. Harv. Univ. **1**(9): 3. Aug. 12, 1933.
TYPE: *Pleurothallis floripecten* Rchb. f.

Leucohyle Klotzsch in Ind. Sem. Hort. Berol. App. 1. 1854.
TYPE: *Leucohyle Warszewiczii* Kl.

Limodorum L. Sp. Pl. ed. 1. **2**: 950. May 1, 1753 (Aug. 16, 1753).
LECTOTYPE: *Limodorum tuberosum* L.
OBSERVATION: Lectotype was chosen by Britton & Brown, Ill. Fl. No. U.S. and Canada, ed. 2. **1**: 562. 1913. This generic name was rejected in 1935 and is a synonym of **Calopogon** R. Br.

Liparis L. C. Rich. Orch. Eur. Annot. 21. Sept. 1817.
TYPE: *Ophrys Loeselii* L.
OBSERVATION: The genus was conserved in 1905, and the type was conserved in 1930.

Lycaste Lindl. in Bot. Reg. **28**: Misc. p. 85, no. 96. Dec. 1842.
TYPE: *Lycaste plana* Lindl.
OBSERVATION: The description of *Lycaste plana* must be regarded as a combined "*descriptio generico-specifica*" according to Article 42 of the *International Code of Botanical Nomenclature*, notwithstanding Lindley's newly published diagnosis in Bot. Reg. **29**: Misc. p. 14. Feb. 1843. The choice of *Lycaste macrophylla* Lindl. by Acuña in Bol. Tec. Cuba **60**: 165. 1939 is incorrect.

Lysimnia Raf. Fl. Tellur. **4**: 143. (July) 1838.
TYPE: *Brassavola cordata* Lindl.
OBSERVATION: This is a synonym of **Brassavola** R. Br.

Macradenia R. Br. in Bot. Reg. **8**: *t. 612*. Mar. 1, 1822.
TYPE: *Macradenia lutescens* R. Br.

Malaxis Soland. ex Sw. Nov. Gen. & Sp. Pl., Prodr. 8. July 1788.
LECTOTYPE: *Malaxis spicata* Sw.
OBSERVATION: Lectotype was chosen by Britton & Brown, Ill. Fl. No. U.S. and Canada, ed. 2. **1**: 570. 1913. The choice of *Malaxis Rheedii* Sw. by Ascherson, Fl. Prov. Brandenb. **1**: 699. Apr. 1864 is incorrect for it was not part of the original protologue.

Masdevallia Ruíz & Pav. Fl. Peru. Prodr. 122. Oct. 1794.
TYPE: *Masdevallia uniflora* Ruíz & Pav.
OBSERVATION: The type was first suggested in Ruíz & Pavón, Syst. Veg. 238. 1798.

Maxillaria Ruíz & Pav. Fl. Peru. Prodr. 116. Oct. 1794.
LECTOTYPE: *Maxillaria ramosa* Ruíz & Pav., *in hoc loco.*
OBSERVATION: A new lectotype is selected here, because the former typifications are incorrect. The choice of *Maxillaria longipetala* Ruíz & Pav. by Acuña in Bol. Tec. Cuba **60:** 171. 1939, is not tenable because of the transfer of this epithet to *Lycaste longipetala* (Ruíz & Pav.)Garay in Caldasia 8: 524. 1962. The choice of *Maxillaria platypetala* Ruíz & Pav. by Brieger and Hunt in Taxon **18:** 602. 1969 is equally untenable for the decision is based on a specimen not part of the original protologue. Brieger and Hunt state that ". . . it is known that Lindley received material from Ruíz and Pavón (Rchb. f. in Bonplandia **4:** 210. 1856) and therefore this specimen could be considered to be at least an isotype of *M. platypetala.*" This argument would be justifiable were it not for Lindley who stated in Hooker, Jour. Bot. **1:** 13. 1834, and in his Genera and Species of Orchidaceous Plants 143. Dec. 1832, that his only specimen was collected by Colonel Hall (*hab. s. sp. comm. cel. Hooker*).

On the other hand, of the 16 species originally assigned to *Maxillaria*, most of which are referable to other genera, there still exists an actual specimen of *Maxillaria ramosa* in the Delessert Herbarium in Geneva, which is part of the original protologue; this was pointed out by Garay in Bot. Mus. Leafl. Harvard Univ. **21:** 259. Apr. 28, 1967. Since this is the only Pavón material which corresponds to *Maxillaria* as it has been used in systematics and horticulture for the last 150 years, it must be chosen as the lectotype for the genus.

Mesadenella Pabst & Garay in Arquiv. Jard. Bot. Rio de Janeiro **12:** 205. 1952.
LECTOTYPE: *Spiranthes esmeraldae* Linden & Rchb. f.
OBSERVATION: Lectotype was chosen by Correa in Darwiniana **11:** 68. 1955. This is a synonym of **Spiranthes** L. C. Rich.

Mesadenus Schltr. in Beih. Bot. Centralbl. 37(2) : 367. Mar. 31, 1920.
LECTOTYPE: *Spiranthes Galeottiana* A. Rich.
OBSERVATION: Lectotype was chosen by Britton & Wilson, Sci. Surv. Porto Rico **5**(2): 186. 1924. This is a synonym of **Spiranthes** L. C. Rich.

Microstylis (Nutt.) Eaton, Man. Bot. ed. 3. 115, 353. Apr. 1822.
TYPE: *Malaxis ophioglossoides* Willd.
OBSERVATION: This generic name was conserved in 1954. It is a synonym of **Malaxis** Soland. ex Sw.

Myrmecophila Rolfe in Orch. Rev. **25:** 50. Mar. 1917.
TYPE: *Schomburgkia tibicinis* Batem.
OBSERVATION: This is a synonym of **Schomburgkia** Lindl.

Myrobroma Salisb. Parad. Londin. **2:** *t. 82*. Sept. 1, 1807.
TYPE: *Epidendrum rubrum* Lamarck.
OBSERVATION: This is a synonym of **Vanilla** Plum. ex Mill.

Narica Raf. Fl. Tellur. 2: 87. Jan.–Mar. 1837.
TYPE: *Neottia acaulis* J. E. Sm.
OBSERVATION: This is a synonym of **Spiranthes** L. C. Rich.

Neocogniauxia Schltr. in Urban, Symb. Antill. 7: 495. Aug. 15, 1913.
TYPE: *Trigonidium monophyllum* Griseb.

Neourbania Fawcett & Rendle in Jour. Bot. 47: 125. Apr. 1909.
TYPE: *Ponera adendrobium* Rchb. f.

Nerissa Raf. Fl. Tellur. 2: 89. Jan.–Mar. 1837.
TYPE: *Neottia glandulosa* Sims.
OBSERVATION: This is a superfluous name and a synonym of **Ponthieva** R. Br.

Nidema Britton & Millspaugh, Bahama Flora 94. June 26, 1920.
TYPE: *Epidendrum Ottonis* Rchb. f.
OBSERVATION: This is a synonym of **Epidendrum** L.

Ocampoa Rich. & Gal. in Ann. Sci. Nat. ser. 3. 3: 31. Jan. 1845.
TYPE: *Ocampoa mexicana* Rich. & Gal.
OBSERVATION: This is a synonym of **Cranichis** Sw.

Octadesmia Benth. in Benth. & Hook. Gen. Pl. 3: 525. Apr. 1883.
TYPE: *Octomeria serratifolia* Hook.
OBSERVATION: This is a synonym of **Dilomilis** Raf.

Octomeria R. Br. in Ait. Hort. Kew. ed. 2. 5: 211. Dec. 1813.
TYPE: *Epidendrum graminifolium* L.

Odontoglossum H. B. K. Nov. Gen. et Sp. Pl. 1: 350. Aug. 1816.
TYPE: *Odontoglossum epidendroides* H. B. K.

Olgasis Raf. Fl. Tellur. 2: 51. Jan.–Mar. 1837.
TYPE: *Cymbidium triquetrum* Sw.
OBSERVATION: This is a synonym of **Oncidium** Sw.

Oncidium Sw. in Vet. Akad. Handl. Stockholm 21: 239. Sept. 1800.
LECTOTYPE: *Oncidium variegatum* Sw.
OBSERVATION: Lectotype was chosen by Garay in Taxon **19:** 444. 1970. This choice corresponds to the guidelines provided in the *International Code of Botanical Nomenclature* for the selection of lectotypes, for this is the only species which Swartz illustrated in detail when he described the genus, and of which the holotype also exists in the British Museum (Nat. Hist.). The choice of *Epidendrum altissimum* Jacq. by Pfeiffer in his Nomencl. Bot. **2:** 497. 1874 is inappropriate for *Oncidium* (*Epidendrum*) *altissimum* (Jacq.) Sw. has been thoroughly misapplied up to the present time. (See Garay & Sweet in Jour. Arnold Arb. **53:** 394, 395. 1972). The choice of *Epidendrum carthagenense* Jacq. by Britton & Wilson, Bahama Flora 97. 1920, is rejected here because no material of the holotype exists.

Onkeripus Raf. Fl. Tellur. 4: 42. (July) 1838.
TYPE: *Maxillaria pallidiflora* Hook.
OBSERVATION: This is a synonym of **Xylobium** Lindl.

Ornithidium Salisb. ex R. Br. in Ait. Hort. Kew. ed. 2. **5**: 210. Dec. 1813.
TYPE: *Epidendrum coccineum* L.
OBSERVATION: The type was suggested by Salisbury in Trans. Hort. Soc. **1**: 293. 1812. This is a synonym of **Maxillaria** Ruíz & Pav.

Ornithocephalus Hook. Exot. Fl. **2**: *t. 127*. Oct. 1824.
TYPE: *Ornithocephalus gladiatus* Hook.

Pelexia Poit. ex Lindl. in Bot. Reg. **12**: sub *t. 985*. June 1, 1826.
TYPE: *Satyrium adnatum* Sw.
OBSERVATION: This generic name was conserved in 1935. It is a synonym of **Spiranthes** L. C. Rich.

Pentulops Raf. Fl. Tellur. **4**: 42. (July) 1838.
TYPE: *Maxillaria decolor* Lindl.
OBSERVATION: This is a synonym of **Xylobium** Lindl.

Physurus L. C. Rich. ex Lindl. Gen. and Sp. Orch. Pl. 501. Sept. 1840.
LECTOTYPE: *Orchis plantaginea* Willd.
OBSERVATION: Lectotype was chosen by Britton & Millspaugh, Bahama Flora 87. 1920. It is a synonym of **Erythrodes** Bl.

Pinelia Lindl. Folia Orch. Pinelia 1. Apr. 30. 1853.
TYPE: *Pinelia hypolepta* Lindl.

Platypus Small & Nash in Small, Fl. SE. U.S. 329. July 1903.
TYPE: *Platypus papilliferus* Small & Nash.
OBSERVATION: This is a synonym of **Eulophia** R. Br.

Platystele Schltr. in Fedde Repert. Sp. Nov. **8**: 565. Nov. 15, 1910.
TYPE: *Platystele bulbinella* Schltr.

Pleuranthium (Rchb. f.) Benth. in Jour. Linn. Soc. Bot. **18**: 312. Feb. 21, 1881.
TYPE: *Epidendrum Dendrobii* Rchb. f.
OBSERVATION: This is a synonym of **Epidendrum** L.

Pleurothallis R. Br. in Ait. Hort. Kew. ed. 2. **5**: 211. Dec. 1813.
TYPE: *Epidendrum ruscifolium* Jacq.

Polyradicion Garay in Jour. Arnold Arb. **50**: 466. July 15, 1969.
TYPE: *Angraecum Lindenii* Lindl.

Polyrrhiza Pfitz. in Nat. Pflanzenfam. **2**(6): 215. Mar. 1889.
TYPE: *Limodorum funale* Sw.
OBSERVATION: This is a synonym of **Dendrophylax** Rchb. f.

Polystachya Hook. Exot. Fl. **2**: *t. 103*. May 1824.
TYPE: *Epidendrum minutum* Aubl.
OBSERVATION: This generic name was conserved in 1905. The correct name of the type species in the genus *Polystachya* is *Polystachya flavescens* (Bl.) J. J. Sm. (See Dunsterville & Garay, Venez. Orch. Ill. **3**: 266. 1965).

Ponera Lindl. Gen. and Sp. Orch. Pl. 113. Aug. 1831.
TYPE: *Ponera juncifolia* Lindl.

Ponthieva R. Br. in Ait. Hort. Kew. ed. 2. 5: 199. Dec. 1813.
TYPE: *Neottia glandulosa* Sims.

Prescottia Lindl. in Hook. Exot. Bot. 2: *t. 115*. Aug. 1824.
TYPE: *Prescottia plantaginea* Lindl.

Prosthechea Knowles & Westcott, Fl. Cab. 2: 111. Sept. 1838.
TYPE: *Prosthechea glauca* Knowles & Westcott.
OBSERVATION: This is a synonym of **Epidendrum** L.

Pseudocentrum Lindl. in Jour. Linn. Soc. 3: 64. Aug. 20, 1858.
TYPE: *Pseudocentrum macrostachyum* Lindl.

Pseudogoodyera Schltr. in Beih. Bot. Centralbl. 37(2): 369. Mar. 31, 1920.
TYPE: *Goodyera Wrightii* Rchb. f.
OBSERVATION: This is a synonym of **Spiranthes** L. C. Rich.

Psilochilus Barb. Rodr. Gen. et Sp. Orch. Nov. 2: 272. 1882.
TYPE: *Psilochilus modestus* Barb. Rodr.

Pterichis Lindl. Gen. and Sp. Orch. Pl. 444. Sept. 1840.
TYPE: *Pterichis galeata* Lindl.

Pteroglossaspis Rchb. f. Otia Bot. Hamb. pt. 1: 67. Apr. 1878.
TYPE: *Pteroglossaspis eustachya* Rchb. f.

Reichenbachanthus Barb. Rodr. Gen. et Sp. Orch. Nov. 2: 164. 1882.
TYPE: *Reichenbachanthus modestus* Barb. Rodr.

Rhynchadenia A. Rich. in Sagra, Hist. Isla Cuba 11: 248. 1841.
TYPE: *Rhynchadenia cubensis* A. Rich.
OBSERVATION: This is a synonym of **Macradenia** R. Br.

Rodriguezia Ruíz & Pav. Fl. Peru. Prodr. 115. Oct. 1794.
LECTOTYPE: *Rodriguezia lanceolata* Ruíz & Pav., *in hoc loco*.
OBSERVATION: Lectotype is chosen here. The holotype of *R. lanceolata* is in the Reichenbach Herbarium in Vienna, and it closely matches the illustrations provided by Ruíz and Pavón, part of the original protologue. Reichenbach already noted this similarity in Bot. Zeit. **10:** 772. 1852.

Rodrigueziopsis Schltr. in Fedde Repert. Sp. Nov. 16: 427. July 31, 1920.
LECTOTYPE: *Rodriguezia eleutherosepala* Barb. Rodr., *in hoc loco*.
OBSERVATION: Lectotype is chosen here. Of the two equally characteristic species referred to this genus by Schlechter, *R. eleutherosepala* is the more common one and specimens referable to it are widely distributed in herbaria. The holotype is Barbosa Rodrigues' original drawing.

Sacoila Raf. Fl. Tellur. 2: 86. Jan.–Mar. 1837.
TYPE: *Neottia aphylla* Hook.
OBSERVATION: This is a synonym of **Spiranthes** L. C. Rich.

Sarcoglottis Presl, Rel. Haenk. 1: 95. 1827.
TYPE: *Sarcoglottis speciosa* Presl.
OBSERVATION: This is a synonym of **Spiranthes** L. C. Rich.

Sauroglossum Lindl. in Bot. Reg. 19: *t. 1618*. Oct. 1, 1833.
TYPE: *Sauroglossum elatum* Lindl.
OBSERVATION: This is a synonym of **Spiranthes** L. C. Rich.

Scaphyglottis Poepp. & Endl. Nov. Gen. ac Sp. Pl. 1: 58. May 28, 1836.
LECTOTYPE: *Fernandezia graminifolia* Ruíz & Pav., *in hoc loco*.
OBSERVATION: Lectotype is chosen here. The holotype is in the Herbarium of Jardín Botánico, Madrid. The choice of *Scaphyglottis parviflora* Poepp. & Endl. by Pfeiffer, Nomencl. Bot. 2: 1068. 1874 is untenable because this epithet was transferred to *Maxillaria* by Garay in Bot. Mus. Leafl. Harvard Univ. 21: 258. 1967.

Schomburgkia Lindl. Sert. Orch. *t. 10*. Apr. 1, 1838.
TYPE: *Schomburgkia crispa* Lindl.

Seraphyta Fischer & Meyer in Bull. Sci. Acad. St. Pétersb. 7: 24. Mar. 10, 1840.
TYPE: *Epidendrum diffusum* Sw.
OBSERVATION: This is a synonym of **Epidendrum** L.

Spathiger Small, Fl. Miami 55. Apr. 26, 1913.
TYPE: *Epidendrum rigidum* Jacq.
OBSERVATION: This is a synonym of **Epidendrum** L.

Specklinia Lindl. Gen. and Sp. Orch. Pl. 8. Apr. 1830.
LECTOTYPE: *Epidendrum lanceola* Sw., *in hoc loco*.
OBSERVATION: Lectotype is chosen here because this species is the one which most approximates the generic characters given by Lindley: "*labellum petalis conforme*," "*sepalis liberis, basi saccatis*." The holotype is in the British Museum (Nat. Hist.). This is a synonym of **Pleurothallis** R. Br.

Spiranthes L. C. Rich. Orch. Eur. Annot. 20. Sept. 1817.
LECTOTYPE: *Ophrys spiralis* L.
OBSERVATION: Lectotype was chosen by Pfeiffer, Nomencl. Bot. 2(2): 1238. 1874, and was conserved in 1930. The choice of *Spiranthes aestivalis* L. C. Rich. by Correll in Fl. Texas 3(3): 169. 1944, is inappropriate. This generic name was conserved in 1905.

Stelis Sw. in Schrad. Jour. Bot. 2: 239. Apr. 1800.
LECTOTYPE: *Humboldtia purpurea* Ruíz & Pav., *in hoc loco*.
OBSERVATION: When Swartz established the genus *Stelis*, he explicitly stated its characters are those given for *Humboldtia* Ruíz & Pav. At the same time he also noted that the generic name *Humboldtia* was previously used by Vahl. Therefore, *Stelis* is merely a new name for *Humboldtia* Ruíz & Pav., and the lectotype for it must be chosen from among the eleven specific epithets provided by Ruíz and Pavón in their *Systema Vegetabilium*. We have found five *Humboldtia* species which are definitely referable to *Stelis*, and of these only *Humboldtia purpurea* exhibits the characters depicted by Ruíz and Pavón on *plate 27* for *Humboldtia*; these drawings are part of the original protologue. The holotype of *Humboldtia purpurea* is in the herbarium of Jardín Botánico, Madrid; duplicates are in the Reichenbach Herbarium, Vienna, and in the Willdenow Herbarium, Berlin.

The generic name *Stelis* was conserved in 1905, although, as Stafleu has

shown in Taxon 8: 258. 1959, the conservation was superfluous at that time. In 1929, *Epidendrum ophioglossoides* Jacq. was selected as the lectotype by Green in Prop. Brit. Bot. p. 100, and this typification was conserved in 1930. Unfortunately, *Epidendrum ophioglossoides* is based on Plumier's polynomial of 1703 as well as on Plumier's drawing of it published subsequently by Burmann in 1759. A closer examination of Plumier's drawing reveals at once that it is referable to the genus *Pleurothallis* R. Br. as we understand it, and is conspecific with *Pleurothallis floribunda* (Lindl.) Lindl.

The above proposed retypification of *Stelis* is necessary to prevent a mass transfer of some 1,000 specific epithets from *Pleurothallis* which is inevitable if the old typification is maintained.

Stellilabium Schltr. Die Orchideen 530. Nov. 28, 1914.
TYPE: *Telipogon astroglossus* Rchb. f.

Stenoptera Presl, Rel. Haenk. 1: 95. 1827.
TYPE: *Stenoptera peruviana* Presl.

Stenorrhynchos L. C. Rich. ex Spreng. Syst. Veg. 3: 677. Jan.–June 1826.
LECTOTYPE: *Neottia speciosa* Jacq.
OBSERVATION: Lectotype was chosen by Britton & Millspaugh, Bahama Flora 86. 1920. The choice of *Satyrium orchioides* Sw. as lectotype by Correa in Darwiniana 11: 70. 1955 is incorrect. Regarding orthography see Sprague in Kew Bull. 243. 1929. This is a synonym of **Spiranthes** L. C. Rich.

Sturmia Rchb. Icon. Bot. Pl. Critic. 4: 39. 1826.
TYPE: *Ophrys Loeselii* L.
OBSERVATION: This is a synonym of **Liparis** L. C. Rich.

Tetragamestus Rchb. f. in Bonplandia 2: 21. Jan. 15, 1854.
LECTOTYPE: *Tetragamestus aureus* Rchb. f.
OBSERVATION: Lectotype was chosen indirectly by Reichenbach in Linnaea 41: 85. 1876, when he transferred *T. modestus* to *Ponera*. The choice of *Scaphyglottis arundinacea* H. Petrop. by Pfeiffer, Nomencl. Bot. 2(2): 1373. 1874 is not correct, for this latter species is not part of the original protologue. This is a synonym of **Scaphyglottis** Poepp. & Endl.

Tetramicra Lindl. Gen. and Sp. Orch. Pl. 119. Aug. 1831.
TYPE: *Cymbidium rigidum* Willd.

Thiebautia Colla in Mem. Soc. Linn. Paris 3: 161. 1824.
TYPE: *Limodorum purpureum* Lamarck.
OBSERVATION: This is a synonym of **Bletia** Ruíz & Pav.

Todaroa Rich. & Gal. in Ann. Sci. Nat. ser. 3. 3: 28. Jan. 1845, not Parlatore 1843.
TYPE: *Todaroa micrantha* Rich. & Gal.
OBSERVATION: This is a synonym of **Campylocentrum** Benth.

Trachelosiphon Schltr. in Beih. Bot. Centralbl. 37(2): 423. Mar. 31, 1920.
LECTOTYPE: *Stenorrhynchus actinosophila* Barb. Rodr.
OBSERVATION: Lectotype was chosen by Acuña in Bol. Tec. Cuba 60: 43. 1939. This is a synonym of **Eurystyles** Wawra.

Trichopilia Lindl. Nat. Syst. Bot. ed 2. 446. May 1836.
TYPE: *Trichopilia tortilis* Lindl.

Trigonidium Lindl. in Bot. Reg. 23: *t. 1923.* Jan. 1, 1837.
TYPE: *Trigonidium obtusum* Lindl.

Triorchos Small & Nash in Small, Fl. SE. U.S. 329. July 1903.
TYPE: *Cyrtopodium ecristatum* Fern.
OBSERVATION: This is a synonym of **Pteroglossaspis** Rchb. f.

Triphora Nutt. Gen. N. Am. Pl. 2: 192. June 1818.
TYPE: *Arethusa trianthophora* Sw.

Tritelandra Raf. Fl. Tellur. 2: 85. Jan.–Mar. 1837.
TYPE: *Epidendrum secundum* Jacq.
OBSERVATION: This is a synonym of **Epidendrum** L.

Tropidia Lindl. in Bot. Reg. 19: sub *t. 1618.* Oct. 1, 1833.
TYPE: *Tropidia curculigoides* Lindl.
OBSERVATION: The type was suggested by Lindley in Wallich's Catalogue No. 7386. 1832.

Tylochilus Nees in Verh. Gartenb. Gesellsch. Berlin 8: 194. *t. 3.* 1832.
TYPE: *Tylochilus flavus* Nees.
OBSERVATION: This is a synonym of **Cyrtopodium** R. Br.

Ulantha Hook. in Bot. Mag. 57: sub *t. 2990.* June 1, 1830.
TYPE: *Neottia grandiflora* Hook.
OBSERVATION: This is a synonym of **Chloraea** Lindl.

Vanilla Plum. ex Mill. Gard. Dict. abridged ed. 4. 3: without page number. Jan. 28, 1754.
LECTOTYPE: *Epidendrum Vanilla* L.
OBSERVATION: Lectotype was chosen by Britton & Millspaugh, Bahama Flora 83. 1920. The correct name of the type is *Vanilla mexicana* Mill. (See Mansfeld in Kulturpfl. Beih. 2: 587. 1959.)

Warczewiczella Rchb. f. in Bot. Zeit. 10: 635. Sept. 10, 1852.
LECTOTYPE: *Warrea discolor* Lindl.
OBSERVATION: Lectotype was chosen by Britton & Wilson, Sci. Surv. Porto Rico 5(2): 214. 1924. This is a synonym of **Cochleanthes** Raf.

Wullschlaegelia Rchb. f. in Bot. Zeit. 21: 131. Apr. 17, 1863.
TYPE: *Cranichis aphylla* Sw.

Xeilyathum Raf. Fl. Tellur. 2: 62. Jan.–Mar. 1837.
TYPE: *Epidendrum altissimum* Jacq.
OBSERVATION: This is a synonym of **Oncidium** Sw.

Xylobium Lindl. in Bot. Reg. 11: sub *t. 897.* July 1, 1825.
TYPE: *Dendrobium squalens* Lindl.

ORCHID HERBARIUM OF OAKES AMES
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THE GENERA OF ZYGOPHYLLACEAE IN THE SOUTHEASTERN UNITED STATES [1]

DUNCAN M. PORTER

ZYGOPHYLLACEAE R. Brown in Flinders, Voy. Terra Austral. 2: 545. 1814, "Zygophylleae"

(BEAN-CAPER FAMILY)

Annual to perennial [often suffrutescent] herbs [shrubs] or occasionally trees; branches usually divaricate, with angled or swollen nodes, growth sympodial. Leaves opposite [occasionally alternate], even-pinnately compound, [sometimes odd pinnate, occasionally simple or 2-foliolate, rarely 3–7-foliolate], often fleshy to coriaceous, persistent, petiolate [to subsessile]; leaflets entire [sometimes lobed], inequilateral, petiolulate to subsessile; stipules paired, free, foliaceous [sometimes fleshy or spinescent], persistent or rarely deciduous to caducous. Flowers [4]5[6]-merous, perfect, hypogynous, regular or occasionally slightly irregular; peduncles terminal or pseudaxillary, 1-flowered, solitary or occasionally few to many. Sepals [4] 5 [6], free or rarely slightly connate basally, imbricate in bud, persistent or occasionally deciduous. Petals as many as sepals, free [rarely connate basally], often clawed, sometimes twisted, imbricate or convolute, deciduous, rarely marcescent. Extrastaminal and/or intrastaminal glandular disc usually present and conspicuous. Stamens in [1] 2 [or 3] whorls of 5 each, outer[most] whorl usually opposite petals, often alternately unequal in length or sterile; filaments free, subulate to filiform [rarely winged], frequently glandular [or appendaged] basally, outer whorl occasionally adnate basally to petals, inserted on or below disc; anthers 2-loculate, subbasifixed to versatile, introrse, longitudinally dehiscent. Gynoecium [2–]5-carpellate, syncarpous; style terminal, usually simple;

[1] This treatment was prepared for a generic flora of the southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of the National Science Foundation (Grant GB–6459X, principal investigator, C. E. Wood, Jr.). The format is that established in the first paper in the series (Jour. Arnold Arb. **39**: 296–346. 1958). The area covered includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with additional material from extraterritorial taxa in brackets. References that I have not seen are marked by an asterisk.

I am very grateful to Dr. Wood for his numerous suggestions and additions, to Mrs. Nancy Dunkly for the preparation of the typescript, and to both for their help in rechecking many of the included references at a time of transition when much of the library of my own institution was not available for consultation. The illustration by Arnold D. Clapman was drawn from materials collected by Dr. Wood, who also made the dissections.

stigma minutely and obscurely lobed to distinctly ridged; ovary superior, [2–]5–10[–12]-lobed and -loculate, sessile or rarely on a short gynophore; ovules 1 or 2 to many in each locule, pendulous [or ascending], anatropous, placentation axile [rarely basal]. Fruit a [2–]5-lobed septicidal [or loculicidal] capsule or a schizocarp splitting lengthwise into 5–10[–12] hard, tuberculate to spiny [or winged] mericarps [rarely a drupe or berry]. Seeds 1 to several [to many] in each locule, endosperm present or absent; embryo with flat cotyledons. TYPE GENUS: *Zygophyllum* L.

Twenty-six genera and about 250 species, widely distributed, but mainly in the warmer, drier regions of the world. Eight genera are represented in North America: *Guaiacum* L., with one native and several cultivated species in southern Florida; *Kallstroemia* Scop., with six native and one introduced species, mainly in the Southwest; *Peganum* L., with *P. mexicanum* Gray native to Texas and *P. harmala* L. introduced into the Southwest from the Old World deserts; *Larrea* Cav., with *L. tridentata* (DC.) Coville widely distributed in the deserts of the southwestern United States; *Porlieria* Ruíz & Pavón, with *P. angustifolia* (Engelm.) Gray in Texas; *Tribulus* L., with two introduced species; and *Zygophyllum* L., with the introduced *Z. Fabago* L. Species of *Guaiacum*, *Kallstroemia*, and *Tribulus* occur in our area.

The Zygophyllaceae are a somewhat isolated family with no close relatives, except perhaps for the Balanitaceae. The family has recently been placed in the Geraniales (Takhtajan, 1959, 1969; Scholz, 1964; Thorne, 1968), Malpighiales (Hutchinson, 1959, 1969, in his Lignosae), and Sapindales (Cronquist, 1968). Airy Shaw (1966) thinks that they are closely related to the Rutaceae; Hutchinson (1969) supposes that they are derived from the Linaceae; and many authors place them near the Erythroxylaceae, Geraniaceae, Oxalidaceae, and other Geraniales *sensu* Engler, but these taxa do not appear to be closely related. The best indication of the families to which they are allied is that of Cronquist (1968), who places them with his Sapindales-Geraniales-Linales-Polygalales complex.

The latest subfamilial classification of the family (Scholz, 1964), follows that originally published by Engler (1890, 1896); It is still a far from satisfactory treatment. The Zygophyllaceae at present are divided into seven subfamilies: Augeoideae Engler (*Augea* Thunb.), Chitonioideae Engler (*Morkillia* Rose & Painter, *Viscainoa* Greene), Nitrarioideae Engler (*Nitraria* L.), Peganoideae Engler (*Malacocarpus* Fischer & Meyer, *Peganum*), Tetradiclidoideae Engler (*Tetradiclis* Stev. ex Bieb.), Tribuloideae D. M. Porter (*Kallstroemia*, *Kelleronia* Schinz, *Tribulopsis* R. Br., *Tribulus*),[2] and Zygophylloideae (*Bulnesia* C. Gay, *Fagonia* L., *Guaiacum*, *Larrea*, *Metharme* Phil. ex Engler, *Miltianthus* Bunge, *Neolue-*

[2] These four genera, which form a natural group within the family, have been discussed in detail elsewhere (Porter, 1969a, pp. 42–46). They deserve recognition as subfamily **Tribuloideae** D. M. Porter, stat. nov. (Based on tribe Tribuleae H. G. L. Reichenbach, Conspectus Regni Veg. 199. 1828.)

deritzia Schinz, *Pintoa* C. Gay, *Plectrocarpa* Gill., *Porlieria*, *Seetzenia* R. Br., *Sericodes* Gray, *Sisyndite* E. Meyer ex Sonder in Harvey & Sonder, *Tetraena* Maxim., and *Zygophyllum*). All but the last appear to be natural taxa, and further study undoubtedly will result in a rearrangement of the Zygophylloideae. Hutchinson (1967) has provided an excellent key to the genera of the family.

Palynological studies (Erdtman, 1952; Agababian, 1964; and Kaligis-Walalangi, 1969) indicate a heterogeneity of pollen types within the family, especially within the Zygophylloideae as recognized above. A combination of data from palynology, comparative anatomy and morphology, and cytology should provide a more rational treatment of this subfamily. Pollen morphology and wood anatomy support the removal of *Balanites* Del. and the recognition of the family Balanitaceae, intermediate between Zygophyllaceae and Simaroubaceae.

Reported chromosome numbers are *Bulnesia Retamo* (Gill.) Griseb. ex Hooker, $2n = 26$ ($x = 13$); *Fagonia* (6 spp.), $2n = 18$, 20, 22, ca. 24 ($x = 9$); *Guaiacum officinale* L., $2n =$ ca. 26; *Kallstroemia pubescens* (G. Don) Dandy in Keay, $2n = 32$; *Larrea* (5 spp.), $2n = 26$, ca. 26, 52, ca. 52 ($x = 13$); *Malacocarpus crithmifolius* (Retz.) C. A. Meyer, $2n = 24$; *Nitraria* (3 spp.), $2n = 18$, 24, 48, ca. 48, 60 ($x = 12$); *Peganum Harmala*, $2n = 22$, 24; *Tribulus* (2 spp.), $2n = 12$, 24, 36, 48 ($x = 6$, 12); *Viscainoa geniculata* var. *pinnata* I. M. Johnston, $2n = 26$; *Zygophyllum* (18 spp.), $2n = 16$, 18, 20, ca. 20, 22, 44 ($x = 8$).

Many studies have been made of the wood anatomy of various taxa in the family. The wood is highly specialized, and the species studied form a distinctive, natural group. The specialized features (cf. Metcalfe & Chalk, 1951, p. 291) are "a vessel member length of 0.1–0.2 mm., storied structure, homogeneous rays and fusiform parenchyma cells, with several other features, such as solitary vessels, diffuse parenchyma and fibres with bordered pits, which are usually associated with an unspecialized structure."

The Zygophyllaceae have many economic uses; Hutchinson (1967, pp. 612, 613) gives a good summary of these (see also *Guaiacum* below). *Kallstroemia hirsutissima* Vail in Small and *Peganum Harmala* are reported (cf. Kingsbury, 1964) to poison cattle, and *Tribulus terrestris* (see below) to poison sheep. Alkaloids have been reported to occur in many genera, and it is these that are suspected in stock poisoning by the species noted above and others in the Old World.

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KEY TO THE GENERA OF ZYGOPHYLLACEAE IN THE SOUTHEASTERN UNITED STATES

General characters: *Nodes angled or swollen; leaves opposite, even-pinnately compound, stipulate; flowers terminal or pseudaxillary, 5-merous, hypogynous, perfect, with an extrastaminal and/or intrastaminal disc.*

A. Plants herbaceous; flowers yellow; stamens unappendaged; fruit a schizocarp separating at maturity into 5 or 10 mericarps.
  B. Fruit tuberculate, at maturity separating into 10 mericarps, beak persistent on receptacle; intrastaminal glands absent. .. 1. *Kallstroemia*.
  B. Fruit spiny, at maturity separating into 5 mericarps, beak falling with mericarps; intrastaminal glands present. ..... 2. *Tribulus*.
A. Plants woody (trees or shrubs); flowers blue or purple; stamens appendaged; fruit a 5-lobed septicidal capsule. ..... 3. *Guaiacum*.

Subfam. TRIBULOIDEAE Porter

1. **Kallstroemia** Scopoli, Introd. Hist. Nat. 212. 1777.

Annual [occasionally perennial] herbs; stems herbaceous [to suffrutescent], diffusely branched, prostrate to decumbent or ascending, terete, somewhat succulent, becoming striate on drying, densely pubescent to glabrate, spreading radially from a central tap root to 1 m. or more long. Leaves opposite, elliptic to broadly obovate, abruptly even-pinnate, one of each pair alternatingly smaller or sometimes abortive; leaflets (2) 3–5 (6)[–10] pairs, opposite, entire, subsessile, elliptic to broadly oblong or obovate, somewhat unequal in size, those on one side of rachis slightly smaller, lowest pair markedly unequal, terminal pair directed forward and more falcate, pubescent to glabrate; stipules foliaceous. Flowers solitary, pseudaxillary, regular; peduncles emerging from axils of alternately smaller leaves. Sepals 5 [6], free, pubescent, persistent [rarely caducous]. Petals 5 [6], white to orange, the same basally or green to brighter than apex, free, spreading (the corolla cuplike), fugacious, [usually] marcescent, convolute. Disc fleshy, annular, obscurely 10[–12]-lobed. Stamens 10 [12], the 5 [6] exterior ones opposite petals, somewhat longer and adnate basally to petals, the 5 [6] opposite sepals subtended abaxially by a small bilobed gland; filaments filiform or subulate [rarely basally winged], unappendaged, inserted on disc; anthers globose or ovoid [to linear-oblong] or rarely linear, those opposite sepals rarely aborting. Style simple, cylindrical to [broadly] conical, more or less 10[–12]-ridged, persisting to form a beak on fruit; stigma capitate or oblong [or clavate], 10[–12]-ridged or -lobed, papillose [rarely coarsely canescent], terminal [rarely extending down almost to base of style]; ovary sessile, 10[–12] -lobed and -loculate, ovoid or pyramidal [globose or occasionally conical], glabrous to pubescent; ovules 1 per locule, pendulous, placentation axile, sometimes 1 or more aborting. Fruit 10[–12]-lobed, ovoid [occasionally conical or rarely pyramidal], glabrous or pubescent, at maturity dividing septicidally and separating from a persistent styliferous axis into 10[–12] or occasionally fewer mericarps; mericarps 1-loculate, 1-seeded, obliquely triangular, wedge shaped, more or less tuberculate or rugose abaxially. Seeds oblong-ovoid, obliquely pendulous; seed coat membranaceous; embryo straight; endosperm absent; germination epigeal. TYPE SPECIES: *Kallstroemia maxima* (L.) Hooker & Arn. (*Tribulus maximus* L.). (Origin of name unknown, although it has been suggested that it is derived from that of Anders Kallström, a contemporary of Scopoli.)

The largest New World genus of the family, with 17 species (see Porter, 1969a), these ranging from Illinois to Argentina, in open, disturbed habitats. Even in the tropics, *Kallstroemia* species invariably will be found in the driest localities of a particular area. Nine species are basically of a southwestern United States-northern Mexican distribution, and the least specialized species of the genus, *K. perennans* Turner, occurs in the Big Bend region of Texas. Three species are basically Caribbean in distribution, and five are South American. Three species occur in our area.

The most common *Kallstroemia* in the Southeast is *K. maxima*. This primarily Caribbean species occurs from Colombia and Venezuela north to Sinaloa, Mexico, on the west, and to South Carolina, on the east, with a waif found as far north as Pennsylvania (Porter, 1970). In our area it has been collected on sandy, disturbed soils near the sea in Florida, Georgia, and South Carolina. It is easily distinguished by its glabrous fruits.

Kallstroemia parviflora Norton has been collected once in Oktibbeha County, Mississippi, where it apparently did not form a persistent colony. It has also been found as a waif in Maryland (Porter, 1970). It is indigenous to grassy, disturbed areas from Illinois, west to Arizona, and south to central Mexico, and it is an introduced weed in Peru. The strigose to glabrous beak on the fruit is two to three times as long as the ovoid, strigose body.

Kallstroemia pubescens (G. Don) Dandy in Keay, $2n = 32$, is known in the United States only from Apalachicola, Florida, where it may or may not have persisted. This basically Caribbean species, known from Peru northward to Sinaloa, Mexico, and the Antilles, was first described from what is now Ghana. It has also been collected in the Ivory Coast and in India (Bennett, 1965). In the Greater Antilles it is known only from Jamaica (Proctor, 1967) and Puerto Rico. The short-pilose to glabrous beak on the fruit is as long as the pyramidal, densely appressed short-pilose body.

Four species grown in the greenhouse have been found to be self-compatible (Porter, 1969a), a decided advantage for weedy plants. They (and apparently all others, except *Kallstroemia perennans*) also can be self-pollinated by an upward and inward movement of the stamens and petals as the flower, which is open in the morning, closes in early afternoon.

Little is known of natural relationships within the genus. The only chromosome number known is that of *Kallstroemia pubescens* (Datta, 1968). Hybridization between *K. maxima* and *K. pubescens*, in Colombia, and between *K. maxima* and *K. Rosei* Rydb. in Vail & Rydb., in Mexico, is suspected (Porter, 1969a).

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Under family references see AGABABIAN; BRAY; BURBIDGE; BURLAGE; COOK & COLLINS; DESCOLE, O'DONELL, & LOURTEIG; ENGLER; ERDTMAN; GÓMEZ DE

LA MAZA; GRAY; HEVLY, MEHRINGER, & YOCUM; KALIGIS-WALALANGI; KINGSBURY; LASSER; MARTIN & DREW; MAURITZON, 1934b; PEREZ ARBELÁEZ; PITTIER; PORTER; ROBBINS, BELLUE, & BALL; VAIL & RYDBERG; and WELKIE & CALDWELL.

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2. **Tribulus** Linnaeus, Sp. Pl. 1: 386. 1753; Gen. Pl. ed. 5. 183. 1754.

Annual or occasionally perennial herbs [very rarely shrubby]; stems herbaceous to suffrutescent, diffusely branched, prostrate to decumbent or ascending, terete, somewhat succulent, becoming striate on drying, densely pubescent to glabrate, spreading radially from a central tap root to 1[–3] m. long. Leaves opposite, elliptical in outline, abruptly even-pinnate, one of each pair alternately smaller or sometimes aborting; leaflets 3–7[–10] pairs, opposite, entire, sessile to very shortly petiolulate, oblong to ovate or elliptical, terminal pair pointed forward, pubescent; stipules foliaceous. Flowers solitary, pseudaxillary, regular; peduncles emerging from axils of alternately smaller leaves. Sepals 5, free, pubescent, caducous. Petals 5, bright yellow or rarely white, darker basally, free, spreading (the corolla cuplike), deciduous, imbricate. Disc fleshy, 10-lobed, annular. Stamens 10, the outer whorl of 5 opposite petals, somewhat longer, and adnate

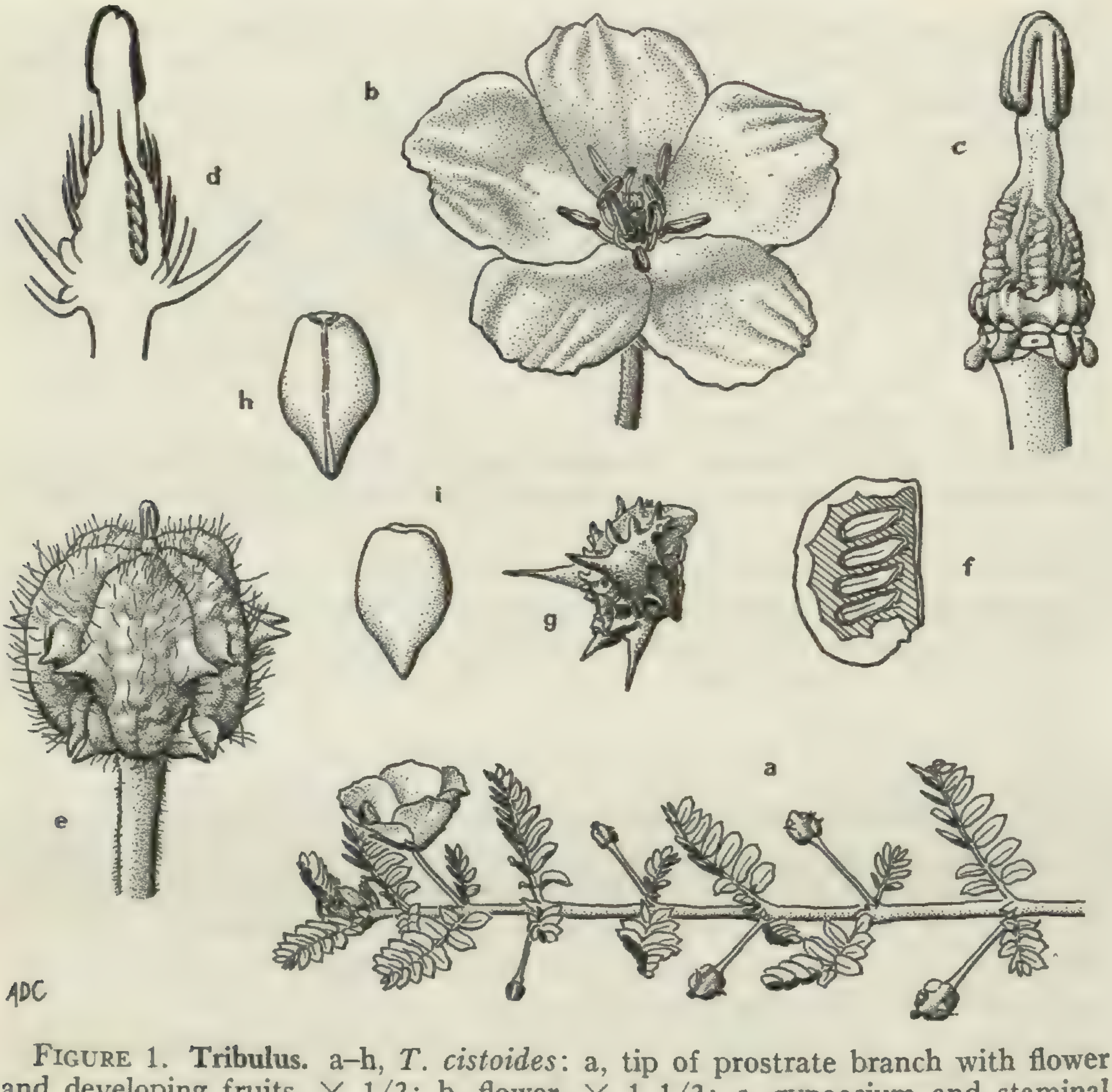

FIGURE 1. **Tribulus.** a–h, *T. cistoides*: a, tip of prostrate branch with flower and developing fruits, × 1/2; b, flower, × 1 1/2; c, gynoecium and staminal glands, the intrastaminal ones united around base of ovary, the extrastaminal ones subtending stamens opposite sepals, the positions of stamens, petals, and sepals unshaded, hairs on ovary not shown, × 6; d, flower in semidiagrammatic vertical section to show placentation and positions of stamens, glands, sepals, and petals — base of sepal and stamen opposite it to left, base of petal and stamen opposite it to right, × 6; e, nearly mature but still green fruit, × 2; f, one mericarp of fruit in median vertical section showing four seeds and embryos, × 2; g, stony part of mature mericarp, softer outer tissues removed, × 2; h, seed, × 6; i, embryo, × 6.

basally to petals, the inner 5 opposite sepals and subtended both ad- and abaxially by nectariferous glands, the intrastaminal glands free or connate to form an urceolate ring surrounding ovary base; filaments filiform or subulate, unappendaged, inserted on disc; anthers cordate to sagittate. Style simple, stout, cylindrical, 5-ridged, deciduous; stigma terminal, pyramidal or globose to inequilateral, 5-lobed, papillose; ovary sessile, 5-lobed and -loculate, ovoid or globose, densely pubescent; ovules 3–5 per locule, pendulous, superposed in 2 vertical rows on placenta, placentation axile. Fruit 5-angled, usually horizontally depressed, pubescent, at maturity dividing septicidally and separating into 5 or rarely fewer mericarps

and leaving no central axis; mericarps broadly triangular, each divided internally by oblique transverse septa into 2–5 one-seeded compartments, spiny [or winged or rarely only tuberculate abaxially]. Seeds oblong-ovoid, obliquely pendulous, horizontally arranged one above the other; seed coat membranaceous; embryo straight; endosperm absent; germination hypogeal. LECTOTYPE SPECIES: *Tribulus terrestris* L.; see Vail & Rydberg, N. Am. Fl. **25**: 109. 1910. (Name from Greek *tribolos*, a kind of caltrop, an iron instrument with four spines arranged so that one always projects upward, used to impede cavalry.) — PUNCTURE WEED, CALTROP, BURR-NUT.

An Old World genus of several dozen species, commonest in Africa and the Near East. Most are weedy occupants of dry, disturbed habitats, either natural or man induced. The spiny mericarps of many species provide an ideal mechanism for dissemination, and man has long been involved in their spread. Three species (two represented in our area) have been introduced into the New World.

Tribulus cistoides L., burr-nut, $2n = 12$, is common in southern Florida, and it is also known from northwestern Florida, Georgia, and Louisiana. Native to tropical and subtropical southern Africa, it is now a weed throughout the drier tropics, mainly in maritime habitats. It is an attractive plant with showy yellow flowers two to four centimeters in diameter that have led to the common name "Jamaica buttercup." The plant is occasionally grown in sandy soils as a garden ornamental or along roads to stabilize shifting soils.

Tribulus terrestris L., puncture vine, is a noxious roadside weed most common in the West and Midwest. In our area it has been collected sporadically in Florida, Louisiana, South Carolina, and Tennessee, and more commonly in Arkansas. It is native to the Mediterranean region, probably to northern Africa. A widespread weed in the warm-temperate areas of the world, it occurs on all continents but Antarctica but has been found only rarely in the tropics. The flowers are one centimeter or less in diameter.

Tribulus cistoides and *T. terrestris* are easily distinguished in the southeastern United States by flower size. In some other areas, however, the flower size of one species may approach or overlap the other, and the morphology of the intrastaminal glands must be relied upon. They are five, triangular, and free in *T. terrestris*, and connate into a five-lobed urceolate ring in *T. cistoides*. A breakdown in the species-specificity of this character in the equatorial Galápagos Islands has led to the hypothesis that hybridization between these two introduced species has taken place there (Porter, 1971a & b).

After trying unsuccessfully for some 50 years to control *Tribulus terrestris* by chemical means, the California Department of Agriculture in 1961 imported two species of weevil from India for biological control. The larvae of both feed selectively on *T. terrestris*, *Microlarinus lareynii* (Jacquelin du Val) on the seeds and *M. lypriformis* (Wollaston) on the

stems. These weevils appear to be well on the way to controlling *T. terrestris* in the Southwest.

In Africa, Australia, and the United States ingestion of the plant by sheep leads to "geeldikkop" or "bighead," a fatal disease involving hepatogenic photosensitization. Both nitrate and selenium poisoning may be involved (see Kingsbury, above).

Diploid ($2n = 12$), tetraploid ($2n = 24$), hexaploid ($2n = 36$), and octoploid ($2n = 48$) races have been reported for *Tribulus terrestris*, but only diploids have been found in *T. cistoides*. According to Malik (1966) the races of *T. terrestris* can be distinguished by pollen and flower size. Chromosome numbers are not known for any other species of this taxonomically difficult and poorly-known genus.

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Subfam. ZYGOPHYLLOIDEAE

3. **Guaiacum** Linnaeus, Sp. Pl. 1: 381. 1753, 'Guajacum'; Gen. Pl. ed. 5. 179. 1754.

Evergreen [deciduous] trees [or shrubs], [1–]2.5–10[–20] m. high, with a dense rounded crown; trunk short, stout, occasionally 1[–2] m. in diameter, the bark thin, light gray [light brown or olive-green], fissured vertically [smooth], separating on the surface into thin whitish [olive-green] scales, the wood hard and resinous, the heartwood dark green or yellow-brown, the sapwood thin and yellow; branches stout, slightly angled, pubescent, becoming glabrate, spreading, the branchlets stout, slightly angled, with conspicuously swollen nodes, green, becoming light gray, fissured, pubescent, becoming glabrate. Leaves opposite [sometimes crowded on short lateral branchlets], even-pinnate, the petiole and rachis pubescent [glabrous]; leaflets [1–]3–5[–7] pairs, opposite, entire, subsessile, [narrowly] elliptic to obliquely oblong or obovate [ovate], rounded [acute to obtuse or retuse] and mucronate apically, inequilateral basally, [membranaceous to] subcoriaceous or coriaceous, pubescent to glabrate, somewhat unequal in size, basal [apical] pair largest; stipules acuminate, usually mucronulate, usually deciduous, sometimes persistent. Flowers showy, solitary to several [or many], slightly irregular by twisting of petals; peduncles borne in axils of minute axillary bracts between stipules [sometimes crowded on short lateral branchlets], shorter than leaves. Sepals 4 or 5, free to slightly connate basally, obovate, pubescent, smaller than petals, deciduous. Petals 4 or 5, blue [violet or rarely white] drying yellow, free, obovate, rounded to lobed apically, clawed and twisted basally, spreading, glabrous or pubescent, imbricate. Disc annular, inconspicuous.

Stamens 8–10, free; filaments subulate or slightly winged basally, unappendaged, inserted on disc; anthers versatile, sagittate or cordate. Style simple, slender, subulate, persisting and forming a beak on fruit; stigma minute, entire or with as many lobes as ovary; ovary on a short gynophore, [2–] 4- or 5-lobed and -loculate, obovoid [obcordate and flattened], glabrous [pubescent]; ovules 8–10 per locule, pendulous, the placentation axile. Fruit a capsule, [2-] 4- or 5-lobed and -winged, obovoid [obcordate and flattened], broadest apically, smooth, glabrous [pubescent], coriaceous, [green] orange to yellowish[-brown], narrowed basally into a short gynophore, septicidally dehiscent. Seeds ovoid, 1 per locule, [1 or 2] 4 or 5 maturing per fruit, surrounded by a thick fleshy red aril; seed coat membranaceous, brown or black; embryo straight, cotyledons foliaceous; endosperm present. LECTOTYPE SPECIES: *G. officinale* L.; see Vail & Rydberg, N. Am. Fl. **25**: 105. 1910. (Name from guayacán, a Caribbean Indian name for species of *Guaiacum* and *Tabebuia* Gomes ex DC. [Bignoniaceae] with extremely hard wood.) — LIGNUM VITAE.

A New World genus of four or five species occurring from Sonora, Mexico, south to Costa Rica and throughout the Caribbean basin north to the Florida Keys and the Bahamas. *Guaiacum sanctum* L., a low gnarled tree rarely up to 10 m. tall, reaches our area on the Florida Keys, where it was formerly of rather common occurrence. With the destruction of the tropical hardwood forests there, the only remaining trees of any size appear to be on Lignumvitae Key. It also occurs in the Bahamas, Cuba, Hispaniola, Puerto Rico, Yucatán, Guatemala, Honduras, Nicaragua, and Costa Rica. The related but quite distinct *G. officinale* L., $2n$ = ca. 26, is indigenous from the Bahamas and Greater Antilles, south through the Lesser Antilles to Tobago, and in Guyana, Venezuela, and Colombia *Guaiacum Coulteri* Gray occurs from northwestern Mexico to Central America, and the closely related *G. unijugum* T. S. Brandegee is endemic to the southern tip of Baja California. Both *G. sanctum* and *G. officinale* are cultivated in southern Florida (and elsewhere in tropical America) for their handsome blue flowers, colorful orange or yellow fruits, and attractive dark green persistent foliage. The violet-flowered *G. Coulteri* is grown to a much lesser extent.

The leaves of *Guaiacum sanctum* have three or four pairs of leaflets, the lowermost and middle pairs being largest, and the fruits are pointed at the apex, are four- or five-lobed and -winged, and have four or five seeds. The leaves of *G. officinale* have two or three pairs of obovate leaflets, with the terminal pair the largest, and the fruits are emarginate or heart shaped at the apex and are two-lobed and -winged with one or two seeds. Both are evergreen plants with flowers 2.5 cm. or less in diameter that are produced as the new foliage is expanding. *Guaiacum Coulteri* has leaves with three to seven pairs of narrowly elliptic leaflets, the middle pairs being largest, and pointed four- or five-lobed and -winged fruits with four or five seeds. The flowers are larger than 2.5 cm. in diameter, and the petals are more dis-

tinctly clawed than in the two preceding species. Flowering usually begins while the plant is leafless before the new leaves unfold.

Guaiacum sanctum and *G. officinale* are sympatric in the Greater Antilles, and *G. sanctum* and *G. Coulteri* are sympatric in Central America. The name *G. guatemalense* Planchon ex Rydb. has been applied to collections from Guatemala, Honduras, Nicaragua, and Costa Rica. However, the range in variation exhibited by these specimens, plus the observation that some have much-reduced seed-set, suggests that *G. Coulteri* and *G. sanctum* are hybridizing and introgressing in Central America.

Guaiacum is closely related to *Porlieria* Ruiz & Pavon, which has about four species, one in Texas and northeastern Mexico and several in southern South America. *Porlieria* differs from *Guaiacum* in having persistent, commonly spinescent stipules; more, smaller, and narrower leaflets; staminal appendages; and two to four ovules per locule. Further study may prove them to be congeneric.

The wood and resin of *Guaiacum* species, especially of *G. officinale* and *G. sanctum*, have long been the most important economic products of the family. Soon after Columbus' voyage to the New World, large quantities of wood were being shipped to Europe because of the supposed medicinal value of an extract of the heartwood. Sold by the pound, the wood was quite expensive, considering that its specific gravity is about 1.2. So many trees and populations have been destroyed that these plants have become extinct or very rare on many of the Caribbean islands. They are very slow growing and are not quick to recolonize areas from which they have been removed.

The name lignum vitae (wood of life) derives from the belief that the wood exhibited miraculous medicinal properties. For over 200 years it was considered a specific remedy for venereal disease. With the invention of steam-powered ships, the wood became important for bearings or bushing blocks to line the stern tubes of propeller shafts. The wood is one of the strongest known, and its high resin content and concomitant self-lubricating properties, combined with its strength, make it ideal for uses under conditions of stress and sea water. Today the wood is used mainly for the manufacture of such turned objects as mallets, pulley sheaves, caster wheels, bowling balls, stencil and chisel blocks, mortars and pestles, brush backs, planes, and the like. For good discussions of the sources of supply, marketing, and uses of lignum vitae, see Record (1921) and Longwood (1962).

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Under family references see Agababian; Asprey & Thorington; Bärner; Bailey & Tupper; Baillon; Bate-Smith; Britton & Shafer; Chattaway; Cook & Collins; Davis; Ehrlich & Raven; Engler; Erdtman; Gómez de la Maza; Gray; Heimsch; Inmadar; Kaligis-Walalangi; Lasser; Martínez; Metcalfe & Chalk; Neal; Perez Arbeláez; Pittier; Porter, 1963, 1969; Record; Record & Hess; Rose; Saunders; Smiley; Tortorelli; Vail & Rydberg; and Williams & Williams.

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on TROPICOS: names, types, syn. & distr

THE GENUS MACROCARPAEA (GENTIANACEAE) IN COSTA RICA

#0006882

RICHARD E. WEAVER, JR.[1]

THE GENUS *Macrocarpaea* (Griseb.) Gilg consists of approximately 30 species of shrubby Gentianaceae with a distribution centered in the Andes of northern South America and extending south and east into the Amazon Basin and the mountains of southern Brazil, and north into the Greater Antilles and the mountains of Costa Rica. Three species are now known from Costa Rica. The most common of these, *M. valerii* Standl., is a familiar summer-blooming shrub of the Cordillera de Talamanca and the Cordillera Central. For nearly 70 years, the second species, *M. subcaudata* Ewan, was represented only by the type collection. A modern collection, from another locality, shows that this plant sometimes grows as an epiphyte. Recently, material of a third species has come to light which is described in this paper as *Macrocarpaea acuminata*.

According to Ewan's (1948) treatment of *Macrocarpaea*, the genus consists of two subgenera: PARANAGENES Ewan, with the herbaceous *M. rubra* Malme from southern Brazil as the sole species; and MACROCARPAEA (*Eumacrocarpaea* Ewan) with two sections based primarily on leaf characters, the typical one (Sect. *Magnoliifoliae* Ewan) and Sect. TABACIFOLIAE Ewan. Of the Costa Rican species, *Macrocarpaea subcaudata* belongs to the typical section while *M. valerii* belongs to Sect. TABACIFOLIAE. However, with its short internodes and relatively small but membranaceous leaves, *M. acuminata* appears to be intermediate between the sections.

In many ways, Ewan's infrageneric classification seems unnatural. Recent work by Nilsson (1968, 1970) has shown that three types of pollen are characteristic of the species included in *Macrocarpaea* by Ewan: a distinctive one, having single grains with a coarse reticulum found in subgen. PARANAGENES as well as in the majority of the species in the typical subgenus, including the three from Costa Rica; another single-grain type with verrucoid processes found in three species of sect. TABACIFOLIAE and characteristic of the monotypic Bolivian *Rusbyanthus* Gilg; and a final type, with pollen in tetrads, found in five species of the typical section and characteristic also of *Chelonanthus* (Griseb.) Gilg, another neotropical genus. Although those species with *Rusbyanthus*-type pollen appear to be referable to *Macrocarpaea* on morphological grounds, those with pollen in tetrads do not. These latter species differ from all the others in that their inflorescence consists of a single, terminal, compound dichasium, the divi-

[1] The author wishes to thank Dr. Robert L. Wilbur of Duke University for collecting and preserving flower buds of *Macrocarpaea valerii*, and the curators of the following herbaria for the loan of specimens: DUKE, F, GH, NY, US.

sions of which are not subtended by foliaceous bracts. The proper generic alignment of these species is unclear, although morphologically they appear most closely related to *Chelonanthus*.

A chromosome number for *Macrocarpaea valerii*, $2n = 42$, is reported here for the first time. The standard squash technique was used and the voucher specimen (*Wilbur 14680*) is deposited in the Duke University Herbarium. The only previous report of a chromosome number in the genus was for the Jamaican *M. thamnoides* (Griseb.) Gilg (Weaver, 1969), also $2n = 42$.

KEY TO THE COSTA RICAN SPECIES OF MACROCARPAEA

A. Leaves subcoriaceous, only the midvein and the primary laterals evident; calyx lobes essentially alike and longer than the tube, minutely spiculate. . . *3. M. subcaudata.*

A. Leaves membranaceous, the lesser veins evident, at least below; calyx lobes unequal, shorter than the tube or rarely equalling it, glabrous.

B. Foliage leaves (those not subtending a flowering branch) 7 cm. broad or narrower, more than twice as long as broad; leaves glabrous or rarely the midvein very sparsely spiculate; corolla 4.4–4.7 cm. long; outer calyx lobes obtuse or acutish, the inner ones rounded, as long as broad or narrower; calyx less than 1/3 as long as the corolla tube; stems smooth; lateral flowering branches in 2 or rarely 3 pairs, unbranched or once branched below the dichasia; stalks of the lowermost flowering branches less than 10 cm. long. . . . . *2. M. acuminata.*

B. Foliage leaves more than 9 cm. broad, less than twice as long as broad; foliage leaves and lower floral leaves spiculate on the veins beneath; corolla 3.0–4.0 cm. long; outer calyx lobes rounded, the inner ones truncate or broadly rounded and broader than long; calyx more than 1/3 as long as the corolla tube; stems papillose (under magnification); lateral flowering branches usually in more than 3 pairs, usually 2–3 times branched below the dichasia; stalks of the lowermost flowering branches more than 10 cm. long. . . . . 1. *M. valerii.*

1. **Macrocarpaea valerii** Standley, Publ. Field Mus. Bot. **18**: 928. 1938.
TYPE. **Costa Rica**: La Hondura de San José, *Valerio 692* (F!).

Sparsely branched shrubs or subshrubs to 4 m. tall. Stems to 3 cm. in diameter, the internodes hollow with age. Foliage leaves broad-elliptic to suborbicular and obovate, abruptly short-acuminate, attenuate or cuneate-attenuate, 17.5–46 cm. long and 9.5–26 cm. broad, the venation very prominent, the 2 upper pairs of primary lateral veins arching into the tip of the leaf; petioles winged, 1.5–6.5 cm. long; leaves subtending the flowering branches smaller, the lowermost orbicular or broad-elliptic, the uppermost ovate and palminerved. Inflorescences terminal and also axillary from the upper nodes, of long-stalked, branched systems of compound or apparently simple dichasia. Pedicels 5–20 mm. long, strongly recurved in fruit. Calyx campanulate, fleshy, 9–14 mm. long, the lobes hyaline-margined and ciliolate, 3–6 mm. long and 3–7 mm. broad, strongly unequal, the

outer ones ovate, the inner ones transversely elliptic to broadly obovate and auriculate at the base. Corolla greenish-white or pale greenish-yellow, campanulate, somewhat fleshy, the lobes recurved, broadly triangular-ovate to nearly semicircular, obtuse to rounded and often notched, minutely ciliolate, 7–12 mm. long and 5–10 mm. broad, the tube 2.2–2.9 cm. long. Filaments 13–18 mm. long, surpassing the corolla tube or not; anthers 3–5 mm. long. Style 13–16 mm. long; stigma deeply bilobed, the lobes oblong-spathulate, ca. 2 mm. long. Capsules 15–21 mm. long, beaked. CHROMOSOME NUMBER: $2n = 42$.

DISTRIBUTION: from 1000–1800 meters in the mountains of central Costa Rica (MAP 1).

REPRESENTATIVE COLLECTIONS

Costa Rica. ALAJUELA: La Pena de Zarcero, *Smith 1001* (F, GH); ca. 19 km. n. of San Ramón, *Wilbur & Stone 10684* (DUKE, US); ca. 4.5 mi. n. of Vara Blanca on Route 9 toward Puerto Viejo, *Wilbur & Stone 10472* (DUKE, US). CARTAGO: Tapantí, *Jiménez M. 2023* (F, GH, NY). HEREDIA: 1.5 mi. n. of Vara Blanca on road to San Miguel, *Weaver 1405* (DUKE). SAN JOSÉ: ca. 12 km. nne. of San Vicente de Moravia on Route 220 in the saddle between Irazú and Barba in the vicinity of La Palma, *Wilbur 14680* (DUKE); Cordillera de Talamanca, Cerro de la Muerte, 16 mi. (by road) n. of San Isidro General, *Webster, Miller, & Miller 12329* (DUKE); 13 km. al nw. de San Isidro del General, *Jiménez M. 2204* (F).

As noted by Ewan (1948), this is the most common of the Costa Rican species of *Macrocarpaea* and is closely related to the Colombian *M. macrophylla* (HBK.) Gilg. In fact, the two are virtually identical, except that the calyx of *M. valerii* is glabrous, while that of *M. macrophylla* is spiculate.

2. **Macrocarpaea acuminata** Weaver, sp. nov. TYPE. **Costa Rica:** Cartago. Tapantí, *Jiménez M. 2023*. (holotype, F; isotypes, GH, NY).

Frutex, ca. 3 m. altus. Folia membranacea anguste elliptica vel elliptico-oblanceolata, apice acuminata, basi attenuata, margine ± revoluta, nervis ± prominentibus, 7–20 cm. longa et 2.5–7 cm. lata, plus duplo longiora quam latiora, glabra vel raro costa sparsim spiculata; petioli ad 1 cm. longi. Inflorescentiae terminales axillaresque, ramis floriferis lateralibus in 2 vel raro 3 paribus oppositis. Calyx 10–12 mm. longus, lobis inaequalibus 5–7 mm. longis et 4–6 mm. latis, longioribus quam latioribus, lobis exterioribus acutiusculis vel obtusis, lobis interioribus rotundatis. Corolla late infundibuliformis 4.4–4.7 cm. longa, tubo 3.2–3.6 cm. longo, calyce plus triplo longiore, lobis recurvatis triangulari-ovatis obtusis ciliolatis ca. 12 mm. longis et 10 mm. latis. Filamenta 20–25 mm. longa, inclusa vel leviter exserta; antherae ca. 6 mm. longae. Stylus 20–25 mm. longus; stigma

MAP. 1. Distribution of the Costa Rican species of *Macrocarpaea.*

profunde bilobata, lobis ca. 3 mm. longis. Capsula 18–22 mm. longa apice rostrata.

Macrocarpaea acuminata is known only from the type locality, where it grows in close proximity to *M. valerii.* Jiménez, who collected both species at Tapantí (*M. acuminata, Jiménez 2023*; *M. valerii, Jiménez 2022*), has noted on the label that what is here called *M. acuminata* may only represent older specimens of *M. valerii.* The two species are similar and are probably closely related, but they may easily be separated by the characters outlined in the key above.

3. **Macrocarpaea subcaudata** Ewan, Contr. U.S. Natl. Herb. 29: 224. 1948. TYPE. **Costa Rica**: [San José.] La Palma, *Wercklé 16492* (holotype, US!; isotype, NY!).

Low shrubs, sometimes epiphytic. Foliage leaves glabrous, narrow-elliptic to oblanceolate, cuspidate-acuminate, long-attenuate, the margins somewhat revolute, 5.4–11.3 cm. long and 1.2–3.0 cm. broad; petioles to 1.5 cm. long. Inflorescences terminal or also axillary from the uppermost node, few-flowered, of long stalked groups of apparently simple dichasia (the dichasia sometimes reduced to single flowers). Pedicels to 7 mm. long or flowers subsessile. Calyx campanulate, minutely spiculate (rather dense in the type collection) or rarely glabrescent, 7–10 mm. long, fused for 1/4–

1/3 its length; calyx lobes essentially alike, ovate to oblong, obtuse or rounded, ciliolate, longer than broad, 5–7 mm. long and 3–4 mm. broad. Corolla cream-colored or somewhat greenish, narrowly campanulate, 3.2–3.4 cm. long, the tube 2.4–2.6 cm. long, the lobes somewhat recurved, triangular-ovate, rounded to obtuse, minutely ciliolate, 8–10 mm. long and 6–8 mm. broad. Stamens inserted at about the middle of the corolla tube, the filaments 17–20 mm. long, slightly surpassing the corolla tube; anthers 3–4 mm. long. Style 15–18 mm. long; stigma deeply bilobed, the lobes oblong-elliptic, ca. 3 mm. long. Capsule unknown.

DISTRIBUTION: at ca. 1500 meters in the mountains east of San José, Costa Rica (MAP 1).

SPECIMENS EXAMINED

Costa Rica. CARTAGO: Rio Grande de Orosí, 8 km. s. of Tapantí, *Lent 934* (F, NY).

Two species of *Macrocarpaea* are now known to be at least partially epiphytic, *M. subcaudata* and *M. browallioides* (Ewan) Robyns & Nilsson from the mountains of central Panama. Unlike the recent collection by Lent, the type collection of *M. subcaudata* bears no notation as to whether or not it was growing epiphytically.

Ewan (1948) considered the closest relatives of *Macrocarpaea subcaudata* to be *M. cerronis* Ewan and *M. salicifolia* from the Guiana Highlands. These species, however, are among those with pollen in tetrads, and, as mentioned earlier, should be excluded from *Macrocarpaea*. Rather, *M. subcaudata* is probably related to *M. acuminata* and to certain of the West Indian species such as *M. pinetorum* Alain and *M. domingensis* Urban & Ekman.

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CYTOLOGICAL STUDIES ON HIMALAYAN MELIACEAE

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THIS WOODY FAMILY is comprised of 52 genera and at least 1,000 species (Styles & Vosa, 1971) distributed throughout the tropics and subtropics of the world. Its importance to forestry rests on several valuable timbers such as the mahogany of the trade (*Swietenia mahagoni* and *S. macrophylla*), mahogany-like African woods, especially of *Khaya* and *Entandrophragma*, and toon of India. Meliaceous woods are prized for furniture and cabinet work. The family is represented in India by 50 species belonging to 18 genera of which 13 species are of commercial importance. *Chukrasia tabularis*, *Toona ciliata*, *T. serrata*, *Melia azedarach*, *M. composita*, *Aphanamixis polystachya* and *Dysoxylum binectariferum* are some of the important timber species studied presently.

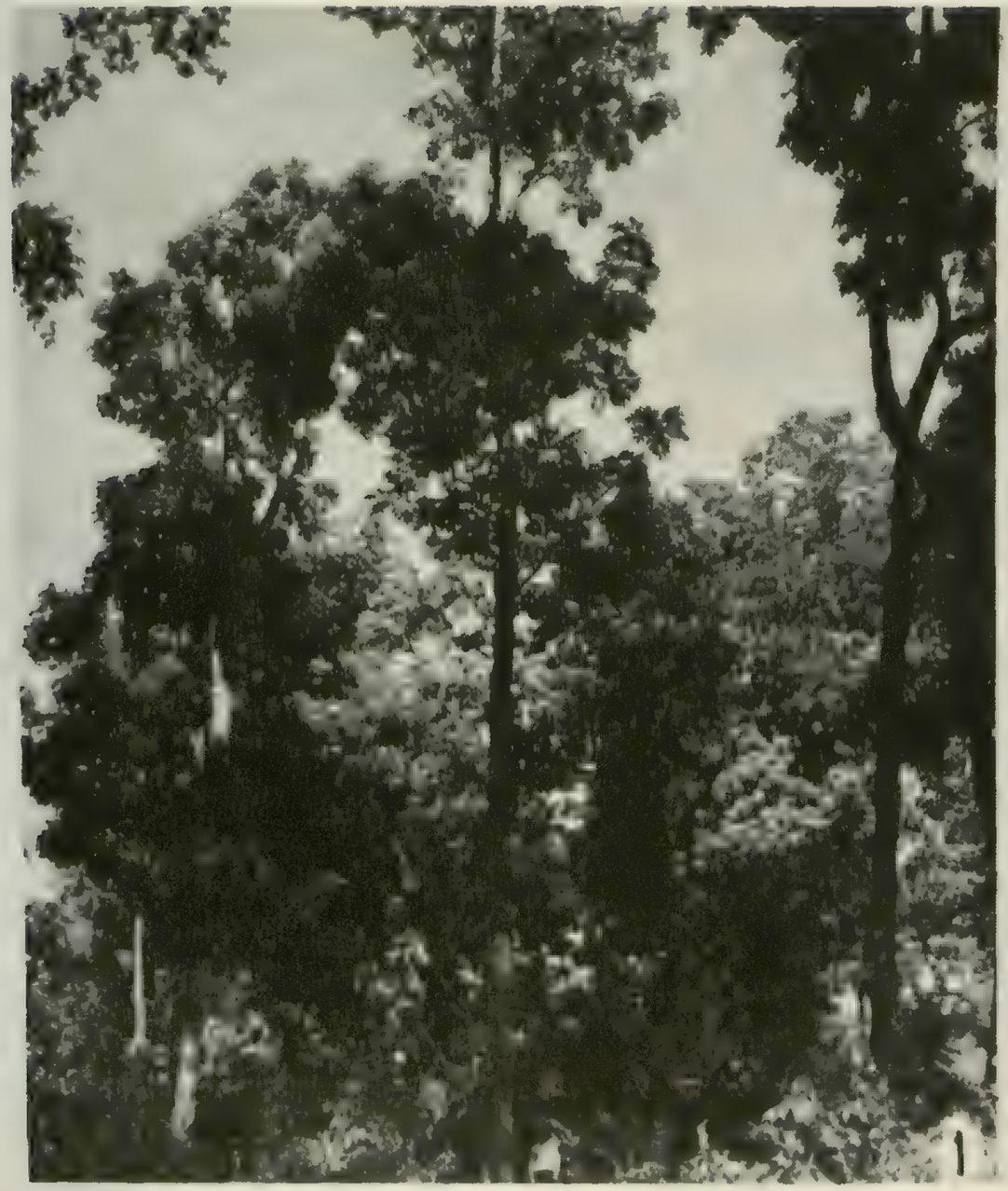
So far about 90 species belonging to 37 genera of Meliaceae have been reported cytologically, the maximum contribution being by Styles and Vosa (l. c.). These authors made mitotic observations with the exception of a single meiotic count. The present work is an attempt to fill lacunae in the cytology of the Himalayan members, chromosome counts for most of which have already appeared in IOPB reports (Mehra & Khosla, 1969; Mehra & Sareen, 1969). Our aim has been not only to know their chromosome counts but especially the process of meiosis, flowering season, and fruiting season, data which are prerequisite for any rational program for the improvement of trees.

MATERIAL AND METHODS

Material was collected from the wild in the forests of the Himalayas and the Khasia and Jaintia hills. Flower buds were fixed in Carnoy's fluid. Squashing of anthers was accomplished in aceto-carmine. For mitotic studies, root-tips were pretreated with .003 M solution of 8-hydroxiquinoline for four hours and squashed in aceto-lacmoid. Figures are at a uniform magnification of × 1360. Voucher specimens have been deposited in the Herbarium, Panjab University, Botany Department, Chandigarh-14 (India).

RESULTS AND DISCUSSION

Chromosome numbers of 24 taxa comprising 18 species belonging to 10 genera are listed in TABLE 1, which also includes data on specific localities of collection, previous counts for the species, and flowering and fruiting seasons. The course of meiosis has been found to be normal in all the taxa.



FIGURES 1 and 2, habit photographs. 1, *Chukrasia tabularis*, a tall tree with straight bole. 2, *Dysoxylum binectariferum*, an individual tree with straight bole.

TABLE 1. List of species studied, supplementary information, and chromosome numbers obtained

NAME	SOURCE	FLOWERING AND FRUITING PERIOD *		CHROMOSOME NUMBER	FIG. NO.	PREVIOUS REPORTS
CHUKRASIA TABULARIS A. Juss.	Darjeeling, Manjitar 300 m.	5–6	9–12	$n = 13$	3	$n = 13$: Rao, 1967
TOONA CILIATA M. J. Roem.	Darjeeling, Teesta 300 m.	3–5	5–8	$n = 28$	4	$n = 28$: Singh, 1951; $2n = 56$: Styles & Vosa, 1971
	Simla, Basantpur 900 m.			$n = 26$	5	
T CILIATA var. PILLISTAMINEA C. DC.	Shillong, Barapani 800 m.	1–2	3–4	$n = 39$	6	
T. SERRATA (Royle) M. J. Roem.	Mussoorie, 1950 m.	5–6	9–10	$2n = 52$	7	
T. MICROCARPA (C. DC.) Harms	Darjeeling, Mahanadi 1500 m.	11–12	2–3	$n = 12$	8	
APHANAMIXIS POLYSTACHYA (Wall.) Parker	Darjeeling, Sukna 150 m.	9–10	2–3	$n = 18$	9	$2n = 72$: Minfray, 1963; Styles & Vosa, 1971
MELIA AZEDARACH L.	Darjeeling, Manjitar 300 m.	3–4	11–2	$n = 14$	10	$2n = 28$: Bowden, 1945; Pathak & Singh, 1949; Minfray, 1963; Gadella et al., 1966; Styles & Vosa, 1971
	Nainital, 1950 m.			$n = 14$		
M. COMPOSITA Willd.	Khasia & Jaintia hills, Garampani, 800 m.	3–4	winter	$n = 14$	11	

M. TOOSENDAN Sieb. & Zucc.	Khasia & Jaintia hills, Garampani 800 m.	5	9	$n = 14$	12	$2n = 28$: Minfray, 1963
AZADIRACHTA INDICA A. Juss.	Darjeeling, Teesta 300 m.	4–5	9–10	$n = 14$	13	$2n = 28$: Pathak & Singh, 1949
	Haldwani, 400 m.			$n = 14$		$n = 14$: Mukherjee, 1952; Deshmukh, 1959
						$2n = 30$: S. & G. Mangenot, 1958; Styles & Vosa, 1971
DYSOXYLUM PALLENS Hiern	Darjeeling, Sukna 150 m.	3–4	7–8	$n = 10$	14	
D. BINECTARIFERUM Hook. f.	Darjeeling, Sukna 150 m.	4–5	winter	$n = 40$	15	
D. HAMILTONII Hiern	Darjeeling, Manjitar 300 m.	10–11	2–3	$n = 40$	16	
D. PROCERUM Hiern	Darjeeling, Lebong 1800 m.	8–10	1–4	$n = 40$	17	
AGLAIA PERVIRIDIS Hiern	Darjeeling, Teesta 300 m.	5–6	12	$n = 20$	18	
A. EDULIS King	Darjeeling, Mahanadi 1500 m.	1–2	3 onwards	$n = 40$	19	
AMOORA WALLICHII King	Darjeeling, Teesta 300 m.	8–10	1–2	$n = 20$	20	
HEYNEA TRIJUGA ROXB.	Darjeeling, Sukna 150 m.; Manjitar, 300 m.	2–4	8 onwards	$n = 14$	21	$2n = 24$: Nanda, 1962; $n = 14$: Rao, 1967
	Nainital, Dogaon 1000 m.			$n = 14$		
CHISOCHETON PANICULATUS Hiern	Darjeeling, Teesta 300 m.	4–8	winter	$n = 23$	22	

* Numbers in this column represent months, e.g., 1: January; 2: February; etc.

Chukrasia A. Juss. includes one or two species distributed from South China to Indo-Malaya. The Indian species *C. tabularis* (FIGURE 1) is a much appreciated timber tree of the Sikkim Himalayas, Assam, the Andamans, Kanara hills of Deccan, Mysore and the western Peninsula. Dark pink blaze and a pink terminal pair of leaflets are diagnostic features for identification in the field. The chromosome count of $n = 13$ confirms Rao's (1967) identical report for the species.

Toona M. J. Roem. is a genus well known for its high grade timbers. *T. ciliata* and *T. serrata* are commercial timbers of India. The former is a morphologically variable tall tree of the tropical Himalayas, also found in central and southern India, which is confined mostly to mixed plain and sal forests. The species shows chromosomal polymorphism and exists in three cytotypes. The haploid count of $n = 28$ in an east Himalayan population agrees with similar findings of Singh (1951) and Styles and Vosa (l. c.). The chromosome numbers of $n = 26$ for a population from the western Himalayas and $n = 39$ for var. *pillistaminea* from the Khasia and Jaintia hills fall in the series of $x = 13$. *T. serrata*, a western Himalayan species with $2n = 52$, is again based on $x = 13$. *T. microcarpa* occurs in the middle hill forests of the Darjeeling hills. It is cytologically interesting in the sense that it adds a new chromosome count, $n = 12$, to the genus.

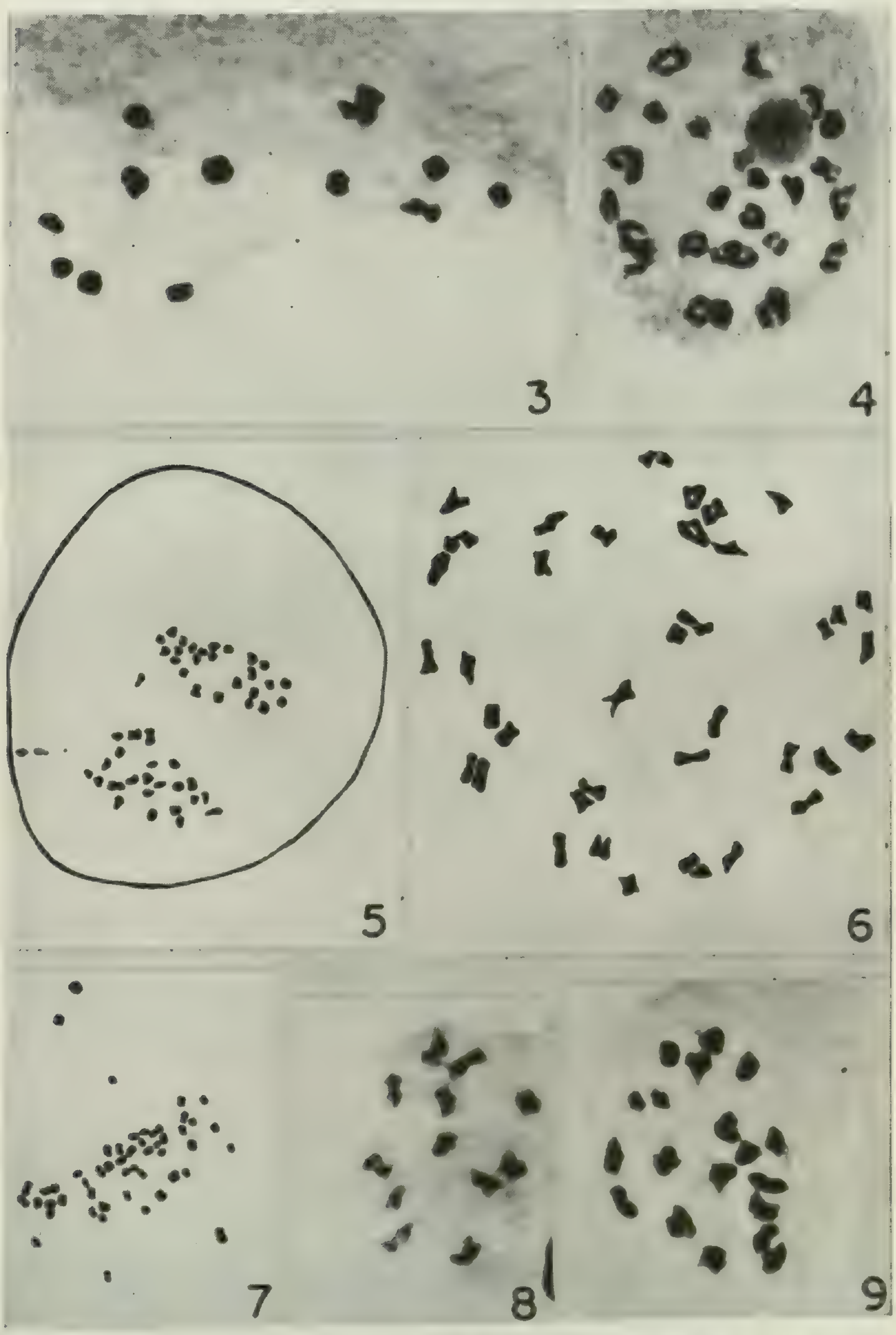
Aphanamixis Blume embraces 25 species, mostly confined to Malaya. The Indian representative, *A. polystachya*, is a medium-sized tree and a commercial timber of the Darjeeling hills. The present taxon having $n = 18$ is diploid, while Minfray (1963) and Styles and Vosa (l. c.) obtained tetraploid counts in this species where $2n = 72$.

Melia L. comprises 15 species. *M. azedarach* and *M. composita*, two Indian timbers, and *M. toosendan* uniformly reveal $n = 14$.

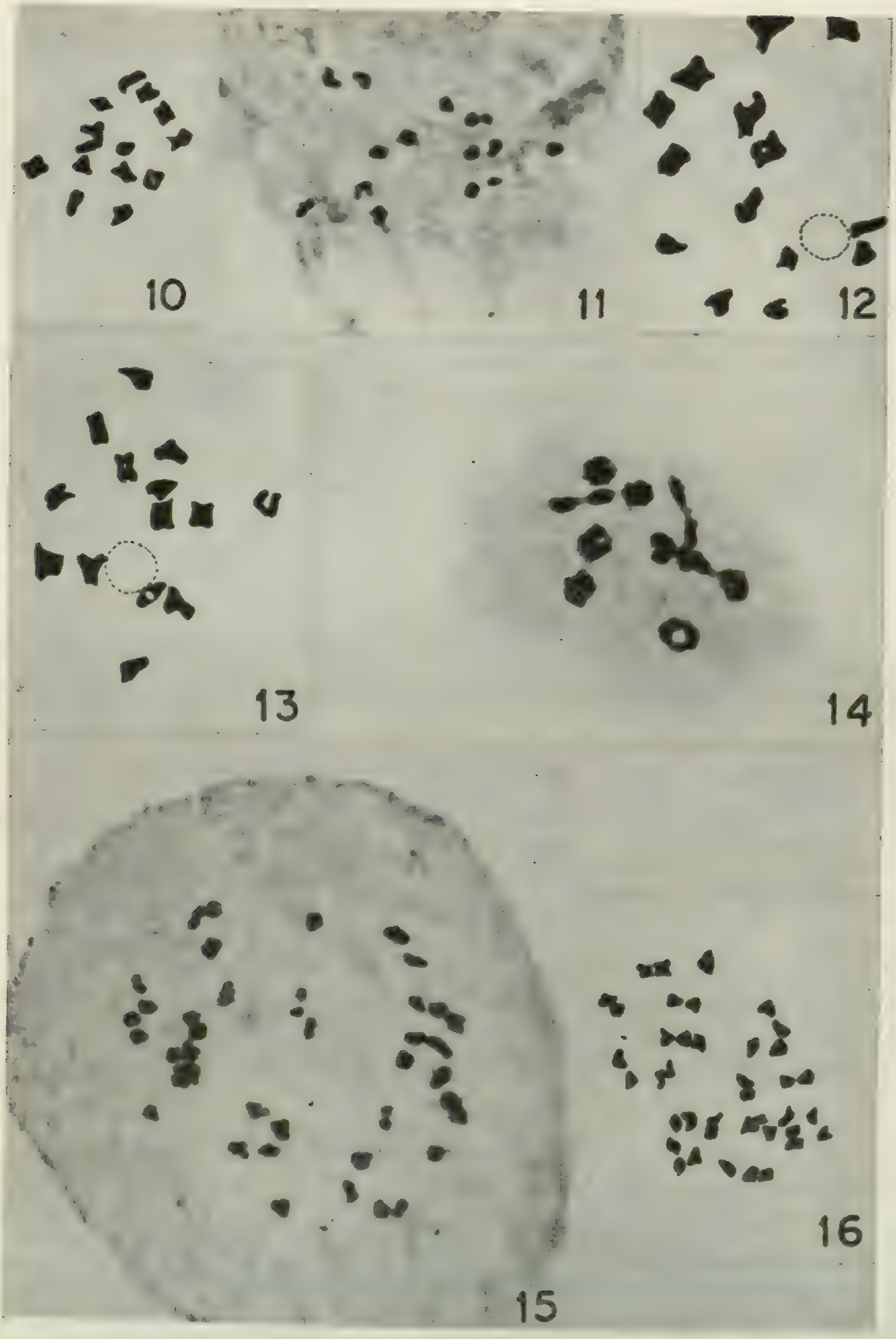
Azadirachta A. Juss. is a small genus of two species. *A. integrifolia* is found in the Philippines, while *A. indica* is widely distributed in the Indo-Malayan region and displays two chromosome numbers, $n = 14$, and $n = 15$ (see TABLE 1); the latter number might have arisen from the former by addition of one chromosome.

Dysoxylum Blume is another Indo-Malayan genus of 200 species of which seven occur in India. Four species which have been studied here are common in the sal and mixed plain forests of the Darjeeling Himalayas. Of these *D. binectariferum* yields timber of economic importance. The counts of $n = 10$ for *D. pallens* and $n = 40$ for *D. binectariferum*, *D. hamiltonii*, and *D. procerum* are the first cytological reports for these species. Other observations on the genus are *D. pachyphyllum* ($2n = 82$: Styles & Vosa, l. c.), *D. ramiflorum* ($n = 36$–38: Paetow, 1931) and *D. spectabilis* ($n = 42$: Beuzenberg & Hair, 1963). Ten is the lowest gametic number recorded in the genus, and it is suggested as the primary base number.

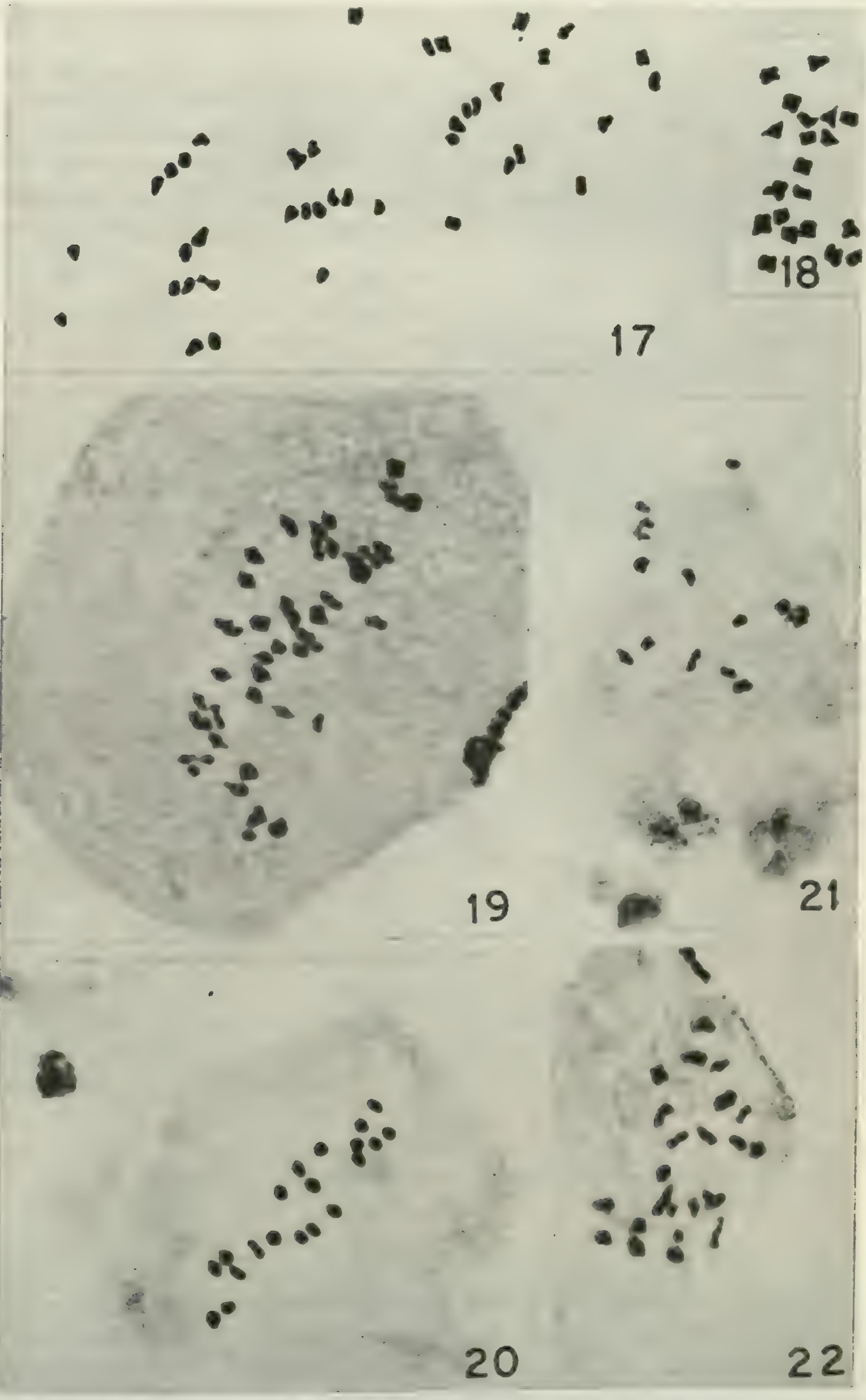
Aglaia Lour. is unimportant from the point of view of forestry. This genus is studied cytologically for the first time here, showing $n = 20$ in *A.*



FIGURES 3–9. **Chukrasia, Toona,** and **Aphanamixis.** 3, *Chukrasia tabularis*, M–I, $n = 13$. 4 and 5, *Toona ciliata*. 4, diakinesis, $n = 28$; 5, A–I, $n = 26$. 6, *T. ciliata*, var. *pillistaminea*, diakinesis, $n = 39$. 7, *T. serrata*, mitotic metaphase, $2n = 52$. 8, *T. microcarpa*, diakinesis, $n = 12$. 9, *Aphanamixis polystachya*, M–I, $n = 18$.



FIGURES 10–16, **Melia, Azadirachta,** and **Dysoxylum.** 10, *Melia azedarach*, diakinesis, $n = 14$. 11, *M. composita*, M–I, $n = 14$. 12, *M. toosendan*, diakinesis, $n = 14$. 13, *Azadirachta indica*, diakinesis, $n = 14$. 14, *Dysoxylum pallens*, diakinesis, $n = 10$; 15, *D. binectariferum*, M–I, $n = 40$; 16, *D. hamiltonii* M–I, $n = 40$.



FIGURES 17–22. **Dysoxylum, Aglaia, Amoora, Heynea,** and **Chisocheton.** 17, *Dysoxylum procerum*, M–I, $n = 40$. 18, *Aglaia perviridis*, M–I, $n = 20$; 19, *A. edulis*, M–I, $n = 40$. 20, *Amoora wallichii*, M–I, $n = 20$. 21, *Heynea trijuga*, M–I, $n = 14$. 22, *Chisocheton paniculatus*, M–I, $n = 23$.

perviridis and $n = 40$ in *A. edulis*. Twenty is suggested as its primary base number.

Amoora Roxb. includes 25 species. *A. wallichii*, a commercial timber, is distributed in India in the moist evergreen forests of the eastern zone and in Andaman. A pink blaze with a few beads of milky juice is a useful field character for its identification. The only species of the genus known cytologically, it shows $n = 20$. It is presumed to be based on $x = 20$.

Heynea Roxb. is comprised of four species only. *H. trijuga* has been consistently observed by us, as well as by Rao (l. c.), to possess $n = 14$ in east and west Himalayan populations. An earlier report of $2n = 24$ by Nanda (1962) appears to be erroneous.

Chisocheton Blume is a genus with 100 species. The single Indian representative, *C. paniculatus*, is a small tree of the mixed plain forests, in Terai, Duars, and the lower hills of Bengal and Assam. This species possesses $n = 23$, which is the only chromosome count for the genus. Twenty-three is the highest base number recorded in the present study.

Unlike most of the other tropical hardwood families, the Meliaceae present a great heterogeneity of chromosome numbers with $2n = 16$, 20, 22, 24, 26, 28, 30, 32, 36, 38, 40, 42, 44, 46, 48, 50, 52, 54, 56, 58, 72, 78, 80, 84, 92, 100, ca. 280, and ca. 360 (cf. Styles & Vosa, l. c.). Evidently, the family has passed through an active phase of numerical chromosomal evolution leading to the delimitation of genera and species. Most of the species possess high chromosome numbers and are in all probability palaeopolyploids that have evolved from ancient extinct ancestors with low base numbers. The original base number of angiosperms is generally believed to lie between 6 and 8, 7 being the most widely presumed number for them, as well as for some primitive tropical woody families like Annonaceae (Raven & Kyhos, 1965) and Proteaceae (Johnson & Briggs, 1963). Approximately 33 percent of the genera of Meliaceae investigated so far fall in the series $x = 14$, although the lowest gametic number is 8, reported only in one instance in *Sandoricum koetjape*. The other commonly represented series seems to be $x = 18$. Both these series are high and could probably have arisen from 7 and 9 respectively. The rest of the numbers encountered in the family can be deduced from these by multiplication, stepwise reduction or addition, or by amphiploidy (FIGURE 23).

SUMMARY

Cytological studies of 18 species belonging to ten genera from the Himalayas have been carried out. Of these, *Chukrasia tabularis* ($n = 13$), *Toona ciliata* ($n = 26$, 28, 39), *T. serrata* ($2n = 52$), *Melia azedarach* ($n = 14$), *M. composita* ($n = 14$), *Aphanamixis polystachya* ($n = 18$), and *Dysoxylum binectariferum* ($n = 40$) are some of the important timber species studied presently. The lowest gametic number in the present studies is reported in *Dysoxylum pallens* ($n = 10$). Normal meiotic be-

havior is characteristic of all presently studied species. The family Meliaceae is known for the extreme polymorphism of chromosome numbers and most of these are palaeopolyploids.

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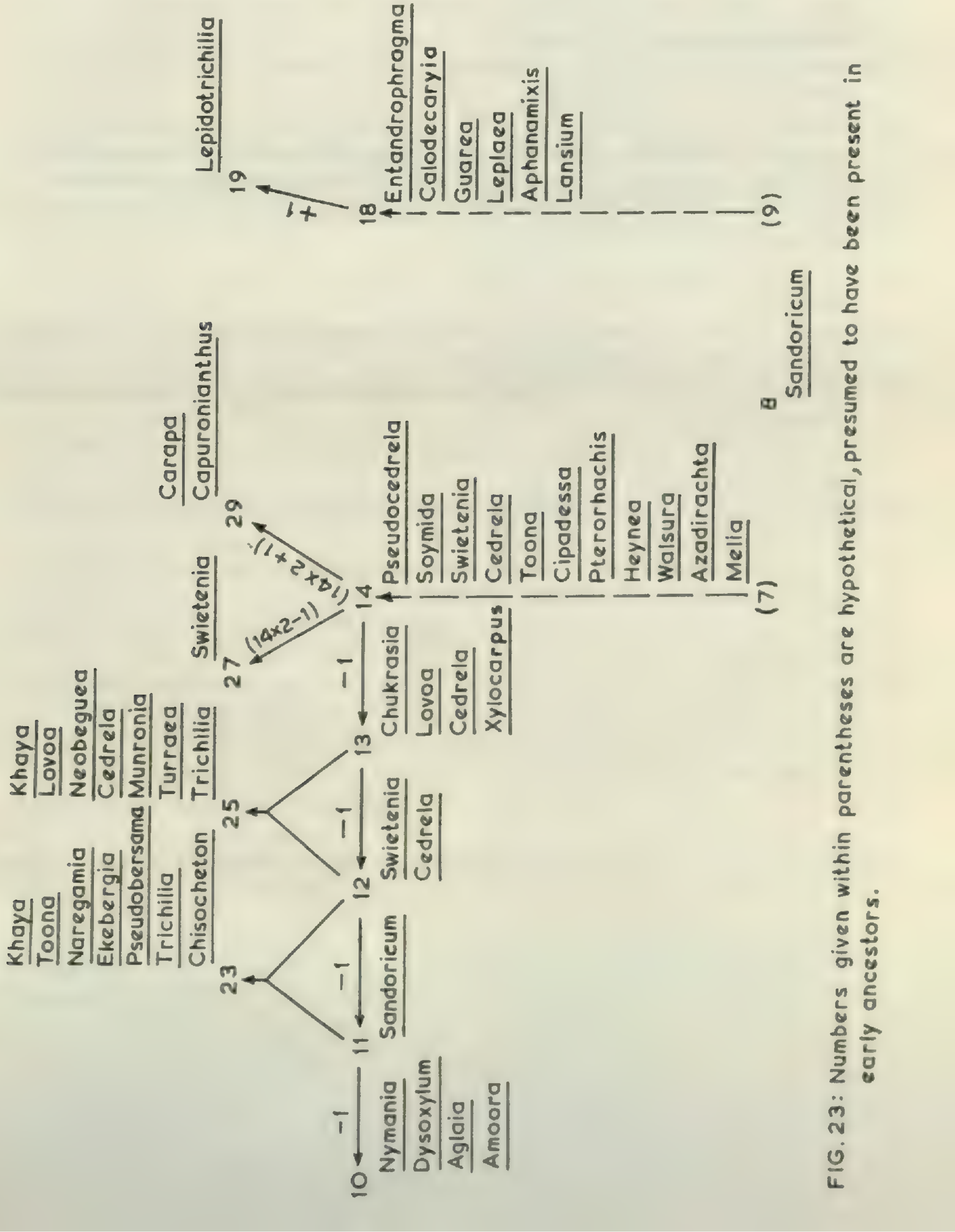

FIG. 23: Numbers given within parentheses are hypothetical, presumed early ancestors.

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